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**Mathematical modelling and conservation applied to army ants**

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# Mathematical Modelling and Conservation Applied to Army Ants

submitted by

Graeme Boswell

for the degree of Ph.D

of the

University of Bath

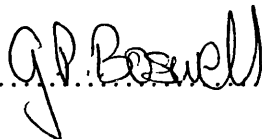
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## Summary

The global rate of species extinction is one million times that of speciation — the Earth is on the brink of another mass extinction. In this thesis we will derive models capable of assessing extinctions and apply them to a keystone member of the tropical rain forest ecosystem — the army ant *Eciton burchelli*. Hundreds of species rely on these ants and therefore they are worthy of conservation.

In §2 we examine habitat fragmentation using analytical patch occupancy and cellular automata models. By appealing to percolation theory and fractal dimension, new and important results are obtained for conservation methods.

Most extinctions are caused by disasters (e.g. climatic events) and yet few models exist capable of incorporating them. In §3 we construct a Markov Chain model and analytical approximations for assessing populations subject to catastrophes and note their inclusion changes the dynamics considerably.

Conservation corridors have long been advocated as the saviour of fragmented environments and have been extensively used throughout the world despite the lack of empirical evidence. In §4 we construct three models, a computer simulation, a Markov Chain model and a Stochastic Differential Equation model to explore corridors and reach novel and important conclusions concerning their use.

In §5 we focus on antbirds — a close associate of *Eciton burchelli*. These birds are undergoing some unusual changes in certain forest remnants which could be reflected around the world. Using two difference equation models — one heuristic, one mechanistic — we examine the causes of these population changes and suggest conservation methods.

Finally in §6 we compare two army ant species who have evolved independently and have contrasting behaviours. Using two size-structured models — one discrete, one continuous — we explain why natural selection has favoured certain characteristics in a particular environment.

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-

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# Chapter 1

## Introduction

During the last 600 million years there have been six mass extinctions (Erwin, 1998), but with the exception of these events, the rates of speciation and extinction have been roughly equal. Today the rate of extinction is one million times greater than the rate of speciation (May, 1990; May et al., 1995); our planet is on the brink of another mass extinction. This extinction, if allowed to occur, will be unlike any previous (Diamond, 1989); there are almost twice as many species present now than prior to the last mass extinction, and also it will be the first not caused by a sudden climatic change, i.e. not caused by a stochastic event, but by gradual (deterministic) environmental degradation. Erwin (1998) states that recovery from mass extinctions depends crucially on the environment, suggesting the effects of the next mass extinction will be unique. Clearly, it is in the interest of the human race to prevent this mass extinction.

May (1990) estimates there are about  $10^7$  species currently alive today (see also Heywood et al., 1994); less than half being recorded — to examine the risk of extinction of all of them is an impossible task, and so we must prioritise (Ginsberg, 1993; Mace, 1994). By conserving certain species, the future of others should be secured. For example, in a simple predator-prey system, one need only make sure there is sufficient prey for the predator to persist (Holyoak and Lawler, 1996). The tropical rain forests are more biodiverse than any other single habitat on Earth and truly constitutes an environment worth saving. This naturally raises the question, what are the important

members (i.e. the keystone species) of the tropical rain forest ecosystem? Whilst certain large carnivores spring to mind and possibly certain bacteria, few people would consider a species of ant, and yet the army ant *Eciton burchelli* is a keystone species whose conservation would immediately guarantee the future for hundreds of other associates. This thesis is primarily concerned with the army ant *Eciton burchelli* and, in particular, mechanisms of reducing its risk of extinction. For the benefit of the reader, a description of *Eciton burchelli* natural history is given in the following section.

## 1.1 Natural History of *Eciton burchelli*

Colonies of *Eciton burchelli* army ants may be found throughout the rain forests of South and Central America (Hölldobler and Wilson, 1990). Numbering in excess of half a million workers and a single queen per colony, they rank among the most spectacular, and most overlooked, of all top level carnivores. They are rare, with an average density of three colonies per square kilometre of rain forest (Willis, 1967; Franks and Fletcher, 1983), but despite this, their impact is massive; indeed at any one time, half of all rain forest is recovering from the effects of their raiding (Franks and Fletcher, 1983). Without this keystone species, the tropical rain forest ecosystem would be thrown into chaos; for example, their prey, other social insects, could escalate to high levels while birds relying on the ants for food would be forced extinct (Willis and Oniki, 1978).

The most studied population of *E. burchelli* is that of Barro Colorado Island (BCI) in Gatun Lake, Panama (figure 1-1). Formally a hilltop, BCI was formed by the flooding of the surrounding valleys during the construction of the Panama canal early in the twentieth century. The island, some 15 square kilometres in area, is completely covered by rain forest and is home to the Smithsonian's Tropical Research Institute. The army ant population on BCI was first observed by T. C. Schneirla in the late 1920s through to the 1960s, by Carl Rettenmayer and Ed Willis during the 1960s, and later by Nigel Franks starting in the late 1970s. Throughout this time, the island has been home to around 50 colonies, and so it is reasonable to assume the population is at equilibrium.

*Eciton burchelli* colonies spend nearly all their time foraging amongst the leaf litter

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### 1.1. NATURAL HISTORY OF *ECITON BURCHELLI*



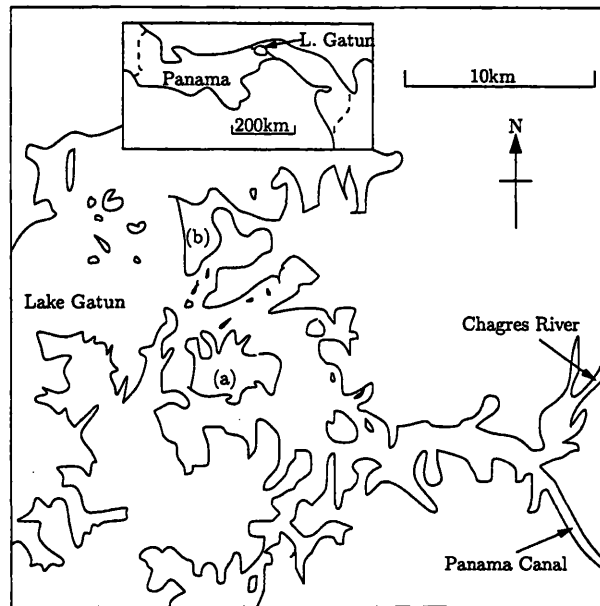


Figure 1-1: Barro Colorado Island in Gatun Lake, Panama. (a) denotes Barro Colorado Island and (b) Juan Gallegos, a peninsula.

on the forest floor, rarely venturing out from the shelter provided by the forest canopy (N. R. Franks, personal correspondence; Willis and Oniki, 1978; Sieving, 1992; Stouffer and Bierregaard, 1995). Although colonies will happily raid across small gaps, larger breaks in the forest canopy are not crossed, so the effects of habitat fragmentation may be great (Boswell et al., 1998).

On most days, a colony sends out a raid from its (temporary) nest site. A single swarm can account for some 200 000 worker ants, and can be up to 200 metres from the nest, though 100 metres is about average. The head of the swarm, resembling a river delta, is about 15 metres wide and steadily moves forward at the rate of 15 metres per hour. Despite this seemingly slow progress, about 30 000 prey items, such as small arthropods and especially other social insects (though not other army ants) are captured in a single day's raiding (Willis, 1967). Upon capture, prey items are carried back to the nest either by individuals or often by teams of workers. *Eciton burchelli* exhibits an incredibly high degree of worker polymorphism. There are in fact four distinct worker castes; from largest to smallest: Majors, Submajors, Medias and

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### 1.1. NATURAL HISTORY OF *ECITON BURCHELLI*

Minors. Whilst the Majors stand at the side of the swarm, protecting their sisters from other predators, the Submajors and the Medias are the main transporters. The Submajors, who generally work on their own, are the main porters, while the Medias often form super-efficient teams of four or five workers who carry disproportionately large amount of prey (Franks, 1986). (That is, if the prey item which is easily handled by the team was evenly broken up between its members, no ant could carry its share.) So, for *E. burchelli* the whole really is more than the sum of the parts.

When observing a swarm raid, one will usually witness the antbirds, a colourful and noisy collection of birds who perch a few centimetres above the raid front and occasionally swoop down to capture prey items flushed out by the swarms, but not the army ants themselves (Willis and Oniki, 1978). These birds depend entirely on the ant swarms for foraging; should *E. burchelli* disappear, the antbirds would swiftly follow along with their associated species, such as antbutterflies (Ray and Andrews, 1980). Antbirds are the subject of chapter 5 and a detailed natural history is given there.

*Eciton burchelli* are not the only army ants found in the rain forests of South and Central America, about 150 different species have been identified and recorded in the literature (Hölldobler and Wilson, 1990). Most of these, however, are column raiders, rather than swarm raiders, and many raid below ground or at night so that inter-specific collisions are rare. On BCI, *E. burchelli* has numerous rivals, especially *Labidus praedator*, the only other common swarm raider (and so is another favourite of the antbirds). However, whilst the diets of these species overlap, there is also a high degree of specialism – for example, *E. burchelli* has a marginally different diet than *L. praedator* (Willis, 1967).

Throughout the year, *Eciton burchelli* army ants exhibit a regular 35-day activity cycle, closely tied in with brood development, consisting of a 21-day statary (or stationary) phase followed by a 14-day nomadic phase (Willis, 1967).

At the start of a statary phase, the single queen lays about 100 000 eggs in a three day period and at the same time larvae in the colony pupate. As there are now fewer mouths to feed, the raids, averaging 119 metres in length, become less frequent;

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### 1.1. NATURAL HISTORY OF *ECITON BURCHELLI*

typically resulting in a colony only raiding every other day. Raiding trails thrown out by the colony from its nest site or bivouac resemble spokes in a bicycle wheel, and indeed, a colony separates neighbouring raids by using a pattern similar to that used by many plants in spiral phyllotaxis (see appendix A, figure 1). Such raiding patterns allow the recovery of arthropod prey along previous raid trails, although the recovery of social insect prey takes much longer, typically about 200 days. After about 17 days in the statary phase, the eggs begin to hatch and new worker ants simultaneously emerge from their pupae. There are now more mouths to feed resulting in the raids becoming more frequent and intense. After approximately 21-days in the statary phase, the raiding becomes so intense, the colony abandons its three-week-home and migrates along the raid trail, thus entering the nomadic phase.

During the nomadic phase, the colony raids every day without fail and on 13 of the 14 days constituting the phase, will in early evening migrate along the raid trail and establish a new nest or bivouac near the end the trail. Typical nest sites include the inside of hollow trees or anywhere offering some sort of shelter. The ants will then link themselves together and form a wall out of their bodies to provide further protection, the queen and her brood being well protected in the midst of this mass of bodies. The following day's raid is usually in a similar direction to the previous, enabling a colony to migrate a considerable distance during this nomadic phase. Typically on one day of the nomadic phase, the colony will raid but not migrate at the end of the day; this probably occurs because the colony encounters a raid trail made by some other colony in the recent past and it knows there will be few prey items around (Franks and Fletcher, 1983). After two weeks on the road, the queen's abdomen starts to swell with the weight of 100 000 eggs, and at the same time the larvae begin to pupate. This triggers the onset of the next statary phase, which is on average some 530 metres (direct overland distance) from the previous statary bivouac (Willis, 1967).

After an area has been raided by army ants, the arthropod levels take only 10 days to recover to pre-raiding densities, most of the recovery occurring through immigration. The main prey items of army ants, other social insects, take much longer to recover,

typically about 200 days (Franks, 1982b). The alternating statary and nomadic phases cause the forest to resemble a mosaic of habitat patches in different stages of ecological succession. In fact, at any one time, half of the forest is recovering from the effects of *Eciton burchelli* occupation (Franks and Fletcher, 1983). Because of its rigid activity cycle, should a colony find itself on a recently raided patch during the statary phase, it is tied to that patch for three weeks, obtaining far less food than it needs, thus causing a major decrease in colony size through starvation. Conversely, a colony finding itself on a patch with high prey densities obtains plenty of food and loses few workers to starvation.

Colony size thus changes as it occupies different quality patches and colony birth and death follow automatically. Colonies die if they become too small or probably if the queen dies, while if they become sufficiently large, give birth to a new colony by a process of binary fission. Franks (1985) showed that colony division occurred precisely at the point where the sum of the growth rates of the two daughter colonies exceeded the growth rate of the parent – this strategy thus minimises the expected time to colony division and maximises the population growth rate.

Colonies who survive to split typically take about three years to do so and the division occurs only during the dry season. When a colony is about to divide, it produces a sexual brood consisting of the usual workers and in addition about 4000 males and six virgin queens. When this sexual brood emerges at the end of the corresponding statary phase, the males, who unlike all other members of the colony can fly, take to the air in search of other *E. burchelli* colonies. The colony then splits in half, usually with the reigning queen heading one half and a virgin queen selected by the worker ants heading the other half. Occasionally, the reigning queen is replaced by a virgin queen, again chosen by the workers. The remaining virgin queens (and maybe the reigning queen) are abandoned by the colony and left to die. The workers' influence does not stop there; they "interview" arriving males (by forcing them to run the gauntlet) and select the best before allowing the queen to mate, which she does at least once in her lifetime and possibly several more times as well (Franks and Hölldobler, 1987). Clearly, there is a

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### 1.1. NATURAL HISTORY OF *ECITON BURCHELLI*

continuous battle between the queen and her workers, which is well documented in the world of eusocial behaviour (Dawkins, 1989; Gotwald, 1995).

## 1.2 Layout Of Thesis

As already mentioned, the majority of this thesis is concerned with extinctions of *Eciton burchelli*. To study this event, we must first model the population dynamics, and then derive some measure of persistence or susceptibility of extinction before examining the resulting models to discover mechanisms of reducing the extinction risk. While the models may at first appear to be very specific to this species, they are derived from the classic principles of Island Biogeography (see, e.g. Andrewartha and Birch, 1954; MacArthur and Wilson, 1967) and in this sense the methods employed to construct the models, if not the entire models themselves, can be applied to most natural populations.

Each chapter addresses a new aspect of the modelling, and for this reason each chapter commences with a statement of the problem it will answer, followed by a brief literature review mentioning similar problems and, if the issues have been previously addressed, how other authors have attempted to solve them. Chapters 2, 3 and 4 follow successively on from one another, while chapters 5 and 6 are entirely independent, but are still concerned in some capacity with *Eciton burchelli*.

Habitat fragmentation is regarded by conservationists as the major cause of species extinction. With the current rate of tropical deforestation at about 150 000 square kilometres per year, fragmentation is becoming an increasingly important issue in tropical rain forests. *Eciton burchelli* is a relatively poor disperser, and so is very vulnerable to habitat fragmentation. In chapter 2, two models are developed to examine how habitat fragmentation effects this important species. The first model is an analytical patch-occupancy model, extending the work of Britton et al. (1996). The analytical model fails to explicitly include spatial effects and so a computer simulation is later developed to examine this aspect. Using percolation theory to examine reserve connectivity, and fractal dimensions to quantify reserve shape, numerous conclusions are obtained, in particular that the current trend for random strip felling ought not to be encouraged.

Parts of section 2.3 have been published in the literature, see Boswell et al. (1998) (reproduced in appendix A) and Boswell et al. (2000) (reproduced in appendix B).

Upon examining all recorded extinctions, there appear to be two causes; a gradual deterministic decrease in species abundance and a sudden catastrophic event removing large numbers of the population simultaneously. It seems strange, then, that modelling catastrophes in population dynamics has been largely ignored. In chapter 3, the affect of catastrophes on populations of *Eciton burchelli* is examined. The colony birth and death rate is first calculated before a new method of examining population distributions under catastrophes is established. The results highlight how the inclusion of catastrophes can dramatically alter the population dynamics. A method formulated by Mangel and Tier (1993) is then applied to *Eciton burchelli* to calculate the expected time to extinction for various reserves under a range of disasters. Again it is seen that catastrophes massively influence population dynamics.

As commented above, habitat fragmentation is regarded as the major cause of species extinction. The classic models of island biogeography, along with the majority of metapopulation models, suggest that species extinction rates can be reduced by connecting habitat patches with a conservation corridor. Such is their intuitive appeal, corridors have been used in many conservation programmes throughout the world. Recently, there have been suggestions in the literature that such constructions may not reduce the risk of extinction, while some authors go even further by claiming corridors can encourage extinctions. In chapter 4 the first evidence that corridors can encourage extinctions is presented. Three models are developed; a computer simulation, a Markov Chain model and a Stochastic Differential Equation model. Across all three models, the expected extinction time is approximated and realistic examples of corridors which reduce population persistence are given. The conclusions are potentially frightening; unless the corridors meet certain criteria relating to the ecosystem they form part of, they could significantly reduce population persistence.

Of the numerous species who associate with the army ants, the ant following birds are probably the most well known. They are entirely reliant on the army ants; fol-

lowing swarming colonies and feeding off insects and arthropods flushed out by the raiding ants. In this century, certain army ant reserves, especially Barro Colorado Island, have seen some unusual changes in antbird diversity. While certain species of antbirds remain as abundant as ever, others have been, or are being, forced extinct in smaller reserves, despite more-or-less constant environmental conditions. It is important to understand the causes of these local extinctions since, given the current rate of tropical deforestation, much of Amazonia will shortly consist of small pockets of forest which may undergo similar population changes, thus implying global antbird extinction. Chapter 5 addresses this important issue by modelling the population dynamics of antbirds. Two models are presented, one a simple heuristic model and a second energy-based mechanistic model. The models suggest a possible cause of the extinctions and from this possible conservation schemes are mentioned.

The cause of gigantism has puzzled philosophers throughout time. Only since Darwin's theory of natural selection can this question be properly answered; species are of a certain size simply because natural selection has favoured species of that size. It is then interesting to consider how different environments favour different characteristics. *Eciton burchelli* is not the only swarm raiding army ant, Africa boasts the Driver ants, such as *Dorylus molestus*. The African army ants have evolved independently of the American army ants and yet share numerous behavioural characteristics. For example, both are swarm raiders, both alternate between nomadic and statary phases and both utilise super-efficient teams in prey retrieval. There are, however, significant differences between species, in particular the difference in average colony size; *Dorylus molestus* colonies are 40 times larger than *E. burchelli* colonies. In chapter 6, this issue is addressed and through two models, one a discrete-size-structured model, the other a continuous-size-structured model, possible reasons are given explaining why natural selection has favoured such drastically different colony sizes in the two different environments.

## Chapter 2

# Habitat Fragmentation

In South and Central America, the tropical rain forests are being destroyed at an alarming rate (Ehrlich and Ehrlich, 1981; Gradwohl and Greenberg, 1988); in Western Europe, urban sprawl devours the countryside every year. All over the world vast areas of natural habitat are being lost and, especially, fragmented each year. This latter trend is worrying since conservationists regard habitat fragmentation as the major cause of species extinction (Simberloff, 1988; Hansson, 1991; Taylor et al., 1993; McCoy and Mushinsky, 1994; Lawton and May, 1995; Hess, 1996b).

For *Eciton burchelli* army ants, the risk of extinction from forest fragmentation is great. Living on the rain forest floor, rarely venturing out of the shelter the forest provides (Willis, 1967, N. R. Franks, personal correspondence), a significant removal of the forest canopy will greatly reduce the amount of accessible habitat having unknown consequences. In this sense, like so many members of the tropical rain forest community, *E. burchelli* is an exceptionally poor disperser and so could be at great risk from fragmentation and deforestation.

In this chapter I first explain typical forest removal strategies, their influence on habitat fragmentation and the various modelling techniques that have been used to understand their effects. An analytical model using mean field (or spatially averaged) dynamics (also known as a patch occupancy model) is then developed to deal with fragmentation, extending the work of Britton et al. (1996). An improved mean field



model is then examined which makes more realistic spatial assumptions. The results of these two models suggests the existence of a critical amount of habitat that can be randomly removed before the army ant population is forced extinct. Such conclusions are typical of fragmentation studies considering random habitat removal. In both models, the explicit inclusion of space is difficult, hence a spatially realistic computer simulation is developed to consider this aspect directly. Initially habitat is randomly removed and it is observed that, similar to the earlier analytical models, there exists a critical amount of habitat that can be removed until army ant persistence becomes impossible. Since this model is spatially realistic, we can appeal to branches of mathematics, such as percolation theory, which considers the behaviour of lattices under random site removal. The model is then examined under correlated habitat removal and it is seen that the manner of habitat loss is important in answering questions on persistence. Finally, the importance of reserve shape on persistence is considered by calculating the fractal dimension of a range of reserves and then an extension of the classic species-area theory is suggested to include reserve shape. This last result makes important suggestions about habitat corridors which are extended upon in chapter 4.

## 2.1 Habitat Loss, Fragmentation and Degradation

Contrary to popular belief, a tropical rain forest is not a stable ecosystem; it is a constantly changing environment (Young and Hubbell, 1991; Hubbell and Foster, 1992; Condit et al., 1992, 1996a). These changes typically occur through habitat loss via natural processes (for example cyclones, forest fires, disease, landslides and tree falls) and the environment is altered by the subsequent habitat recovery (Condit et al., 1996b). However, these natural processes are now of minimal influence when compared to human deforestation, such as that caused by logging, road building, mining and large scale clearing for cattle pasture and other agricultural crops (Ehrlich and Ehrlich, 1981). Whilst traditional societies practised slash-and-burn cultivation, where only small areas of land were cleared which could recover quickly, today large scale clearing occurs in nearly all rain forests and is of such that several hundred years would need to pass

for the forest to return to anywhere near its original state (Stouffer and Bierregaard, 1995).

Since the 1970s the rate of tropical deforestation has accelerated greatly (Repetto and Gillis, 1988; Balmford and Long, 1994). The Eastern region, in places such as Australia, Sumatra and Malaysia, began to suffer huge losses due to timber and agricultural operations (Gillis, 1988). Amazonia, which became a focus of world attention, was being cleared mostly for large cattle ranches and ambitious government programmes, such as colonisation along the Transamazon Highway. Total rates of tropical deforestation are difficult to estimate, but probably somewhere around 150,000 sq km of rain forest are destroyed or seriously degraded every year (Balmford and Long, 1994). Some unique rain forests have been almost totally destroyed. For example, there remains less than two per cent of the original Atlantic coastal rain forest of Brazil (Repetto, 1988).

Loss of biodiversity and global warming (due to increased levels of carbon dioxide) became global issues surrounding rain forest destruction. It now seems clear, however, that the loss of species is by far the more important concern. So little is yet known about rain forest diversity and ecology that large-scale extinctions could take place as a result of human activities before anything can be done to understand their consequences, and more importantly, prevent them from happening. It is for precisely this reason that mathematical models must be developed, in order to both predict and prevent such extinctions.

### 2.1.1 Modelling Habitat Fragmentation

The first mathematical model of habitat fragmentation was Richard Levins' metapopulation (a population of populations) model (Levins, 1969, 1970); it being derived from the principles of island biogeography (MacArthur and Wilson, 1967). The classic Levins' metapopulation model considers a large number of identical habitat patches which are either occupied by a certain species or are empty. Each occupied patch is assumed to become extinct at rate  $e$  and send out colonisers at rate  $c$ , spatial effects being ignored. Thus if  $p$  denotes the proportion of occupied patches, the rate at which the

metapopulation emits colonisers is  $cp$  and the probability a single coloniser successfully restarts a population is  $1 - p$ , so that Levins' model is

$$\frac{dp}{dt} = cp(1 - p) - ep. \quad (2.1)$$

This model has two steady states,  $p = 0$  corresponding to metapopulation extinction, and possibly another at  $p = 1 - e/c$ , as long as  $c > e$ . The main prediction of Levins' model is that metapopulation persistence is possible if and only if the extinction rate is less than the colonisation rate. Numerous studies have extended Levins' model to deal with species competition and habitat removal (e.g. Hanski, 1991; Diekmann, 1993; Aldaz, 1994; Andr  n, 1994; Tilman et al., 1994; Moilanen and Hanski, 1995; Gonzalez et al., 1998): two classic studies are those of Lande (1987) and Nee and May (1992).

Lande (1987) extended Levins' model by setting a proportion of the habitat patches to be unsuitable for occupation. He then proceeded to show that the steady state proportion of occupied patches  $p^*$  satisfied

$$p^* = \begin{cases} 1 - \frac{1-k}{h} & \text{if } h > 1 - k \\ 0 & \text{otherwise} \end{cases}$$

where  $k$  is termed the *demographic potential* which depends upon the individual's life-time distribution and birth rate and  $h$  denotes the proportion of patches suitable for occupation. Notice that if too much habitat is removed (i.e.  $h$  becomes sufficiently small), persistence becomes impossible. This model is then extended to consider edge effects (which then leads Lande to calculate a minimum island size for existence of a population) and stochastic fluctuations in the life history parameters, but the general conclusions remain unchanged.

Nee and May (1992) consider two species in competition, one a superior competitor, the other a superior disperser. A differential equation model based around (2.1) is constructed. Habitat patches are then removed and it is discovered that the inferior competitor can increase in abundance whilst the superior competitor is forced extinct. Once more there exist critical parameter values corresponding to species persistence

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## 2.1. HABITAT LOSS, FRAGMENTATION AND DEGRADATION

and extinction.

The major drawback of Levins'-type models is that they do not consider space explicitly (but see Rand, 1994). They assume mean field dynamics, or spatially averaged dynamics; local interactions and dynamics may be important to the behaviour of the system as a whole. Furthermore, population size in each habitat patch, which is often ignored, may be important. For example, the "Rescue Effect", as initially described by Brown and Kodric-Brown (1977), (see also Gortelli, 1991) suggests that patch extinction rates for small populations can be reduced by the arrival of potential colonisers from other patches. There are essentially two different methods of including population size in metapopulation models; either by allowing the patch-populations to change size discretely or continuously. In the first instance, one introduces new classes of patches which correspond to the different population levels which may occur on a patch, thus turning Levins' model (2.1) from a single equation into a system of ordinary differential equations. Of course, this also increases the number of parameters in the model whose estimation is often difficult (see, for example, Hanski, 1991). The second method of incorporating population size is to assume patch populations vary continuously (Hastings and Wolin, 1989; Hastings, 1991). The rate each patch goes extinct and the rate each patch omits colonisers can be expressed and a model consisting of a system of PDEs is constructed describing the population of a single patch and the entire metapopulation. Such models contain many parameters and are also very complicated to analyse.

For these reasons, a different class of models has been developed – individual-based simulations called cellular automata (e.g. Caswell and Etter, 1993; Durrett and Levin, 1994; Dytham, 1994; Travis and Dytham, 1998). Here the habitat (usually) consists of regularly sized and spaced patches occupied by populations of varying sizes. Rules are then specified as to how the system evolves over time; for example, how empty patches are colonised and how populated patches become extinct. It is then easy to consider habitat removal simply by removing patches from the simulation (e.g. Lavorel et al., 1993). The simulation can then be run and both short and long-term behaviour observed.

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### 2.1. HABITAT LOSS, FRAGMENTATION AND DEGRADATION

The major advantage of cellular automata models is their ability to explicitly include spatial arrangement. In many models, the patches are just the elements in a square lattice (see, for example, Lavorel et al., 1993; Durrett and Levin, 1994; Dytham, 1994; Bascompte and Solé, 1996) and the removal of squares (which corresponds to habitat destruction) is easily considered. As patches are removed, the shape and behaviour of the lattice changes resulting in changes of the biological system. Certain branches of mathematics, e.g. percolation theory, are particularly well suited to such a situation but as yet no study has connected this with a real biological system (but see O'Neill et al., 1992; Lavorel et al., 1993; With and Crist, 1995, who have considered theoretical populations).

## 2.2 An Analytical Model of Habitat Fragmentation

In this section we extend a published analytical model of *Eciton burchelli* army ants to consider the influence of habitat removal. Initially the model considers only mean field (or spatially averaged) dynamics; spatial effects are largely ignored. The model is then extended by allowing only limited dispersal so that space is more rigorously included.

### 2.2.1 The Model of Britton et al. (1996)

Britton et al. (1996) (see also Partridge et al., 1996; Britton et al., 1999) constructed a model for the population dynamics of *Eciton burchelli* army ants. Their model was in essence a discrete time patch-occupancy predator-prey model. A patch was chosen to be a square section of rain forest having side 180 metres, being roughly the area raided by a single colony during the statary phase. Each patch had either high or low densities of prey, depending upon whether the patch had been raided by an army ant colony in the previous  $n$  time steps (one time step representing a single 35-day activity cycle). Thus a patch of age less than  $n$  (one that has been raided in the last  $n$  time steps) has low prey levels, whilst a patch of age greater than or equal to  $n$  has high prey densities. Ant colonies were classified into  $2m - 1$  size classes, one unit of size corresponding to about 60 000 worker ants. At the end of each time step, every colony would choose

to move to another patch, either at random (mean field dynamics) or within a local neighbourhood (improved mean field dynamics); multiple patch occupancy was not allowed. Should the colony land on a young patch, one of age less than  $n$ , the prey densities will be low, there will be little food, and so the colony will decrease one unit in size. Conversely, should an old patch be chosen, prey will be plentiful and the colony grows by one size unit. It is assumed in the model that the nomadic phase has minimal effect on colony dynamics compared to the statary phase, since a colony briefly passes through a range of habitat patches, rather than occupy a single patch for a significant time interval. Colonies decaying to size 0 are assumed to have died while those reaching size  $2m$  split into two colonies of size  $m$  – this mimics the dynamics observed in the field (Franks, 1985). We summarise here the results of Britton et al. (1996):

- The proportion of occupied patches for the mean field model is  $1 - (1/2)^{(1/n)}$ , in good agreement with the field data
- The improved mean field model predicts slightly lower abundance than the mean field model — a better approximation with the field data
- One half of the habitat at any one time is recovering from the effects of army ant raiding, agreeing with the field data
- Colony size is triangularly distributed with mean  $m$  — remains to be tested, but mean colony size appears reasonable.

In the remainder of this section we shall extend this model to consider the effect of rain forest destruction, corresponding to patch removal in the model. Hartshorn (1989, 1995) describes so-called ‘sustainable’ logging strategies which involve randomly felling strips of rain forest of areas comparable to the patches in the model so the problem is a biologically important one.

### 2.2.2 A Mean Field Model With ‘Bad’ Patches

As mentioned in section 1.1, *Eciton burchelli* colonies are very reluctant to venture out of the shelter provided by the rain forest and so when a nomadic colony encounters a

habitat patch devoid of canopy cover, the colony will retrace its route of emmigration. We thus introduce the concept of a ‘bad’ patch which could correspond to an area of felled rain forest. At the end of an activity cycle, a colony chooses to move another patch; should this patch be ‘bad’, the colony will be forced to spend the next time step on the same patch as it spent the previous. In this sense a ‘bad’ patch is bad since choosing it means that the colony is forced to reraid a recently raided area and therefore decrease in size.

To be consistent with the model of Britton et al. (1996), we make use of the following notation:

- $x_i^t$  denotes the proportion of patches occupied by a colony of size  $i$  at time  $t$
- $y_j^t$  denotes the proportion of patches of age  $j$  at time  $t$  (Recall, the age of a patch is the time since it was last raided.)
- $x^t := \sum_{i=1}^{2m-1} x_i^t$  denotes the proportion of patches occupied by a colony of any size at time  $t$ .
- $y^t := \sum_{j=0}^{n-1} y_j^t$  denotes the proportion of young patches at time  $t$  (i.e. those patches of age less than  $n$ )
- $y_b$  denotes the proportion of ‘bad’ patches which are randomly distributed around the reserve.

Clearly, since patches of age 0 are those currently occupied,

$$x^t = y_0^t. \quad (2.2)$$

Furthermore, since any patch is either removed or able to be occupied,

$$y_b + \sum_{j=0}^{\infty} y_j^t = 1 \quad \forall t.$$

Define  $p^t$  to be the probability a colony makes a favourable move (i.e. onto an old patch) at time  $t$  and write  $q^t = 1 - p^t$  as the probability of an unfavourable move at

time  $t$  (i.e. onto a young or removed patch). Then we have the following Markov Chain model describing the colony dynamics:

$$\begin{aligned}
x_1^{t+1} &= q^t x_2^t \\
x_2^{t+1} &= p^t x_1^t + q^t x_3^t \\
x_3^{t+1} &= p^t x_2^t + q^t x_4^t \\
&\vdots \\
x_{m-1}^{t+1} &= p^t x_{m-2}^t + q^t x_m^t \\
x_m^{t+1} &= p^t x_{m-1}^t + q^t x_{m+1}^t + 2p^t x_{2m-1}^t \\
x_{m+1}^{t+1} &= p^t x_m^t + q^t x_{m+2}^t \\
&\vdots \\
x_{2m-2}^{t+1} &= p^t x_{2m-3}^t + q^t x_{2m-1}^t \\
x_{2m-1}^{t+1} &= p^t x_{2m-2}^t.
\end{aligned} \tag{2.3}$$

We can acquire useful information from this Markov chain by defining the expected colony size on a patch to be

$$z^t := \sum_{k=1}^{2m-1} k x_k^t.$$

Multiply the  $k^{\text{th}}$  row of (2.3) by  $k$  and add the resulting equations to obtain

$$z^{t+1} = p^t(z^t + x^t) + q^t(z^t - x^t).$$

Evaluating this expression at equilibrium (i.e. with  $x^t = x^{t+1} = x^*$  and  $z^t = z^{t+1} = z^*$ ), recalling that  $p^* + q^* = 1$ , gives rise to the trivial equilibrium

$$x^* = 0 \tag{2.4}$$

and the non-trivial solution

$$p^* = \frac{1}{2}. \tag{2.5}$$



The probability a colony migration is unfavourable is simply the probability that either a young or a 'bad' patch is chosen, which in the mean field approximation is simply the sum of the proportions of young and removed patches. Thus we have that  $q^* = y^* + y_b$  where  $y^*$  represents the proportion of young patches at equilibrium. From equation (2.5) we hence derive that

$$y^* = \frac{1}{2} - y_b. \quad (2.6)$$

Notice that since  $y^*$  is a proportion and hence non-negative, the metapopulation persists if and only if

$$y_b < \frac{1}{2}. \quad (2.7)$$

This restriction shall be commented on later.

Now consider the patch equations. A patch of age  $j > 0$  at time  $t + 1$  must have been of age  $j - 1$  at time  $t$ , and moreover, this patch will have escaped occupation at time  $t + 1$ . Since the probability of any patch escaping occupation at time  $t$  is  $1 - x^t$ , we arrive at the patch equations

$$y_j^{t+1} = y_{j-1}^t (1 - x^{t+1}) \quad \forall j \geq 0, t > 0. \quad (2.8)$$

Evaluating (2.8) at equilibrium and using the boundary condition provided in (2.2) yields

$$y_j^* = (1 - x^*)^j x^*. \quad (2.9)$$

From the definition of  $y^*$  and invoking (2.9),

$$\begin{aligned}
 y^* &= \sum_{j=0}^{n-1} y_j^* \\
 &= x^* \left( 1 + (1 - x^*) + (1 - x^*)^2 + \cdots + (1 - x^*)^{n-1} \right) \\
 &= 1 - (1 - x^*)^n.
 \end{aligned} \tag{2.10}$$

Upon substituting (2.6) into (2.10) and combining with (2.4), the condition which yields the trivial solution, gives

$$x^* = \begin{cases} 1 - (\frac{1}{2} + y_b)^{1/n} & \text{if } y_b < 1/2 \\ 0 & \text{otherwise.} \end{cases} \tag{2.11}$$

Stability of the equilibria may be determined by numerical calculation of the eigenvalues of the Jacobian corresponding to equation (2.3). In all cases examined, if  $y_b < 1/2$  the non-trivial equilibrium is stable while the trivial steady state is unstable. For values of  $y_b > 1/2$  the only steady state  $x = 0$  is stable.

Figure 2-1 illustrates how the population density for this mean field model varies as a function of the proportion of ‘bad’ habitat.

### 2.2.3 An Improved Mean Field Model With ‘Bad’ Patches

We shall now extend on the mean field approximations of above and consider space explicitly by using an *improved mean field* model. In reality, a colony can only move a limited distance during the nomadic phase – recall, this is governed by the egg laying cycle of the queen. In *Eciton burchelli* army ants, the average distance between two successive statary phase bivouacs is 530 metres, and so in the mathematical model it corresponds to a colony in one square migrating to any of the 24 squares on the edge of a  $7 \times 7$  square whose centre is the current position; see figure 2-2. This implies the transition probabilities in the Markov Chain (2.3) are different under more realistic spatial assumptions.

A given patch thus has a neighbourhood of attainable sites, let this number be  $M$ ,

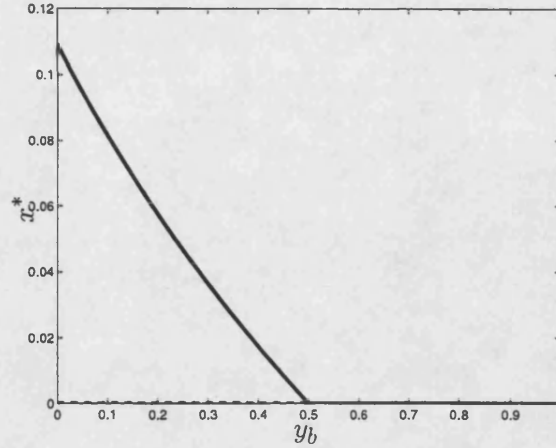


Figure 2-1: The steady state populations  $x^*$  are plotted as a function of the parameter  $y_b$ , the proportion of ‘bad’ patches. The solid line denotes stable equilibria while the dashed line denotes unstable steady states. Values of  $y_b$  less than  $1/2$  yield non-trivial equilibria but for  $y_b \geq 1/2$  persistence is impossible. This implies an environment can have a maximum number of permanently degraded patches before it is unable to support any *Eciton burchelli* colonies.

of which  $M(1 - y_b)$  are habitable (i.e. not ‘bad’). Let us write  $N(A)$  to denote the neighbourhood of a patch  $A$  and  $y(S)$  to be the mean field proportion of young patches in a set  $S$  (so  $y(N(A))$  is simply the number of young patches in the neighbourhood of  $A$  divided by  $M$ ). Notice that if  $A$  is currently occupied, the colony at  $A$  must have arrived from somewhere in the neighbourhood of  $A$ ; thus at least one patch in  $N(A)$  is habitable; but this yields no information about the remaining  $M - 1$  patches. However, if  $A$  is currently unoccupied, this says nothing about any of the  $M$  patches in  $N(A)$ . Hence the mean field proportion of young patches in the set  $N(A)$  is dependent upon whether  $A$  is currently occupied or empty. To this end, let the mean field  $y_j(N(A))$  of patches of age  $j$  in the neighbourhood of the patch  $A$  satisfy

$$y_j(N(A)) = \begin{cases} y'_j & \text{if } A \text{ is occupied} \\ y''_j & \text{if } A \text{ is unoccupied} \end{cases}$$

where  $y'_j$  and  $y''_j$  are independent of  $A$ . By definition, the mean of the neighbourhood

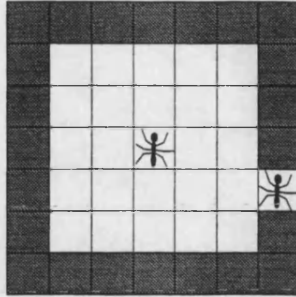


Figure 2-2: A colony occupying one square will try to move to any of the 24 squares on the edge of a 7-by-7 square whose centre is the current position (assuming none of these patches are ‘bad’).

mean fields is the total mean field, which leads to

$$y_j = x^* y'_j + (1 - x^*) y''_j \quad \forall j \geq 0. \quad (2.12)$$

Let us consider the mean field of patches of age 0, i.e. those currently occupied. Suppose patch  $A$  is currently occupied. There must then exist a patch  $B \in N(A)$  which the colony currently at  $A$  arrived from and patch  $B$  will have age 0 if and only if it is currently occupied. Let  $x$  denote the probability that  $B$  is now occupied. No information is known about the remaining  $M - 1$  patches in  $N(A)$  however long  $A$  has been occupied in succession by the same colony, and so we shall treat them as being no different than patches surrounding an unoccupied patch (which we also know nothing about, as stated above). Thus

$$y'_0 = y''_0 \left(1 - \frac{1}{M}\right) + \left(\frac{x}{M}\right). \quad (2.13)$$

An alternative approach would have been to assume the condition of the  $M - 1$  patches in  $N(A)$  other than patch  $B$  was typical of that found throughout the domain, and therefore replace the “no information” term with a weighted average. Mathematically this could correspond to replacing  $y''_0$  in (2.13) with a term such as  $xy'_0 + (1 - x)y''_0$  which is clearly an improvement on saying we know nothing special about these  $M - 1$  patches in  $N(A)$ . For simplicity, however, we shall keep with equation (2.13).

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## 2.2. AN ANALYTICAL MODEL OF HABITAT FRAGMENTATION

Now consider the mean field of patches of age 1. If  $A$  is currently occupied then there exists a patch  $B \in N(A)$  from which the colony arrived. The age of patch  $B$  will depend on two things: firstly the length of time  $A$  has been inhabited by the same colony in succession, and secondly what happened at  $B$  since the colony on it left for  $A$ . We thus require the probability  $\mathbb{P}(B \text{ is age } 1 | A \text{ is age } 0)$  which clearly depends upon the number of ‘bad’ patches selected by the colony currently at  $A$ . With probability  $1 - y_b$  the colony at  $A$  will have been there for 1 cycle and not yet attempted to move. In this case, patch  $B$ , from which the colony at  $A$  just arrived, will be of age 1 if and only if  $B$  is unoccupied this time step (with probability  $1 - x$ ). If the colony at  $A$  has been there for  $j$  cycles (with probability  $y_b^j$ ), patch  $B$  will be of age 1 only if it is empty this cycle but was occupied during the previous time step (with probability  $x(1 - x)$ ). Thus

$$\begin{aligned} \mathbb{P}(B \text{ is age } 1 | A \text{ is age } 0) &= (1 - y_b)(1 - x) + y_b x(1 - x) + y_b^2 x(1 - x) + \dots \\ &= \frac{(1 - x) [(1 - y_b)^2 + x y_b]}{1 - y_b}. \end{aligned}$$

We have no information about the remaining  $M - 1$  patches in  $N(A)$  and so treat them as being no different from patches surrounding an empty patch. Hence

$$y'_1 = y''_1 \left(1 - \frac{1}{M}\right) + \frac{1}{M} \frac{(1 - x) [(1 - y_b)^2 + x y_b]}{1 - y_b}. \quad (2.14)$$

Finally consider the mean field for patches of age  $j > 1$ . If  $A$  is currently occupied then there will be a patch  $B \in N(A)$  from which the colony arrived. The age of patch  $B$  will depend on the length of time  $A$  has been occupied by the same colony in succession and what happened at  $B$  since the colony on it left for  $A$ . We thus require  $\mathbb{P}(B \text{ is age } j | A \text{ is age } 0)$ . If the colony currently at  $A$  has been there for  $j$  time steps (with probability  $y_b^j$ ),  $B$  will be of age  $j$  with probability  $(1 - x)^j$ . Alternatively, patch  $B$  may be of age  $j$  if it was last occupied by another colony  $j$  times steps ago other

than the one currently at  $A$  (which has been there for at least  $j$  cycles). Thus

$$\begin{aligned}\mathbb{P}(B \text{ is age } j | A \text{ is age } 0) &= y_b^j(1-x)^j + y_b^{j+1}x(1-x)^j + y_b^{j+2}x(1-x)^j + \dots \\ &= \frac{(1-x)^j y_b^j [xy_b + 1 - y_b]}{1 - y_b}.\end{aligned}$$

The remaining  $M-1$  patches are of unknown ages and are treated as being no different from those surrounding an unoccupied patch. Thus

$$y'_j = y''_j \left(1 - \frac{1}{M}\right) + \frac{1}{M} \frac{(1-x)^j y_b^j [xy_b + 1 - y_b]}{1 - y_b} \quad \forall j \geq 2. \quad (2.15)$$

Eliminating  $y''_j(N)$  from equations (2.13)–(2.15) by using (2.12) yields

$$\begin{aligned}y'_0 &= y_0 \left(\frac{1 - \frac{1}{M}}{1 - \frac{x}{M}}\right) + x \left(\frac{\frac{1-x}{M}}{1 - \frac{x}{M}}\right) \\ y'_1 &= y_1 \left(\frac{1 - \frac{1}{M}}{1 - \frac{x}{M}}\right) + \frac{(1-x)[(1-y_b)^2 + xy_b]}{1 - y_b} \left(\frac{\frac{1-x}{M}}{1 - \frac{x}{M}}\right) \\ y'_j &= y_j \left(\frac{1 - \frac{1}{M}}{1 - \frac{x}{M}}\right) + \frac{(1-x)^j y_b^j [xy_b + 1 - y_b]}{1 - y_b} \left(\frac{\frac{1-x}{M}}{1 - \frac{x}{M}}\right) \quad \forall j \geq 2.\end{aligned} \quad (2.16)$$

Summing the equations in (2.16) from  $j = 0$  to  $n-1$ , defining  $y' := \sum_{j=0}^{n-1} y'_j$ , results in the mean field of young patches around an occupied patch as

$$\begin{aligned}y' &= y \left(\frac{1 - \frac{1}{M}}{1 - \frac{x}{M}}\right) + \left(\frac{\frac{1-x}{M}}{1 - \frac{x}{M}}\right) \left\{ x + \frac{(1-x)[(1-y_b)^2 + xy_b]}{1 - y_b} \right. \\ &\quad \left. + \frac{[xy_b + 1 - y_b]}{1 - y_b} ((1-x)^2 y_b^2 + \dots + (1-x)^{n-1} y_b^{n-1}) \right\}.\end{aligned} \quad (2.17)$$

Thus, by defining

$$\begin{aligned}P &= \frac{1 - \frac{1}{M}}{1 - \frac{x}{M}} \\ Q &= \frac{\frac{1-x}{M}}{1 - \frac{x}{M}} \left\{ x + \frac{(1-x)[(1-y_b)^2 + xy_b]}{1 - y_b} \right. \\ &\quad \left. + \frac{[xy_b + 1 - y_b]}{1 - y_b} ((1-x)^2 y_b^2 + \dots + (1-x)^{n-1} y_b^{n-1}) \right\},\end{aligned}$$

the probability a colony chooses an unfavourable patch (i.e. either a young or 'bad' patch) is thus

$$q = Py + Q + y_b \quad (2.18a)$$

and the probability the move is favourable is then just

$$p = 1 - q. \quad (2.18b)$$

Substituting the transition probabilities of (2.18) into the Markov Chain (2.3) describes the changes in colony size for the improved mean field approximation.

Notice that equations (2.2), (2.3) and (2.17) with (2.18) constitute a dynamical system whose equilibria are  $x_i^*$  and  $y_j^*$ . This system has been solved numerically for various values of  $M$  and  $n$  and the non-trivial steady states appear to be stable. Figure 2-3 shows how the density of *Eciton burchelli* colonies varies as a function of  $y_b$ , the proportion of 'bad' patches for numerous values of  $M$ . It is seen that there exists a critical proportion of removed patches (for  $M = 24$  which is typically the case for *Eciton burchelli*,  $y_b \approx 0.46$ ) where army ant persistence becomes impossible. Notice there is a strong qualitative agreement with this improved mean field model and the earlier mean field approximation, but that quantitatively this improved mean field approximation predicts extinction will be caused by less habitat destruction than the former. As one would expect, in the limit as  $M \rightarrow \infty$ , this improved mean field model tends to the mean field model of earlier.

The destruction of habitat may also be considered using the improved mean field model of above by varying  $M$  – the number of patches in the neighbourhood. The effect of habitat destruction may be to reduce the options of a colony in choosing its next patch in which to spend the statary phase; so rather than being able to initially choose from any of 24 patches as typically considered by the model (fig. 2-2), the colony may only be able to choose from some number less than this. Figure 2-3 considers such cases and plots the equilibrium number of colonies in a reserve as a function of the

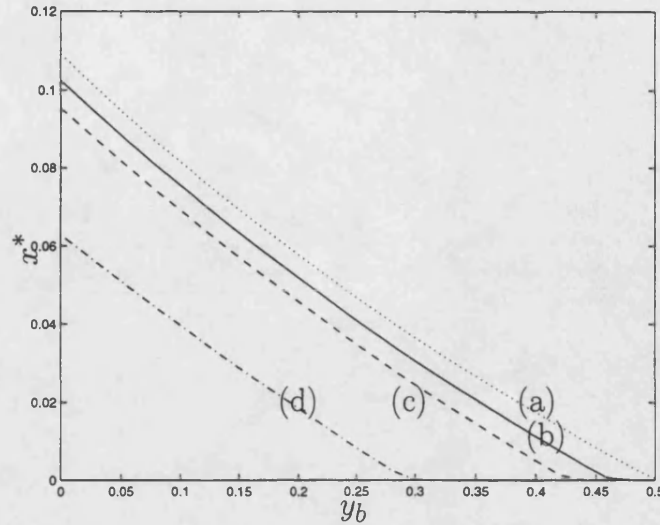


Figure 2-3: The stable equilibrium population densities  $x^*$  are plotted as a function of  $y_b$  for a range of dispersal kernels  $M$  with  $n = 6$ . (a) shows the case for  $M = 1 \times 10^5$  which is close to mean field model of earlier (c.f. figure 2-1). (b) considers  $M = 24$ , the most likely case for *Eciton burchelli*. Notice that for values of  $y_b < 0.46$  persistence can occur whilst extinction is the only equilibrium for  $y_b > 0.46$ . (c) shows  $M = 12$  and (d)  $M = 4$ , both could also correspond to habitat removal (see text). In the last two cases it is clear that by limiting the ability of the army ants to disperse, the initial mean field model breaks down and extinctions are easily caused by considerably smaller amounts of habitat removal.

proportion of 'bad' patches for various values of  $M$ . It is seen that decreasing  $M$ , i.e. removing habitat, significantly reduces the population size. Further to this, the critical value of  $y_b$  is reduced as  $M$  decreases.

#### 2.2.4 Discussion of Mean Field Models: Implications for Conservation

The mean field and improved mean field models both predict the existence of a critical amount of habitat that can be randomly removed before persistence becomes impossible. Such conclusions have been reached by numerous other authors for a variety of biological systems (e.g. Lande, 1987; Nee and May, 1992; Andrén, 1994; McCoy and Mushinsky, 1994; Tilman et al., 1994; Dytham, 1995a; Moilanen and Hanski, 1995; Gosselin, 1998; Hernández-Suárez et al., 1998). From a conservation viewpoint, these



results suggest that random strip felling, as is encouraged at the moment (Hartshorn, 1989, 1995), can be successful only if a small amount of habitat is at any one time unsuitable for *Eciton burchelli*. However, if the strips are narrow enough (for example, comparable in size with tree fall gaps) then problems will be lessened, but commercial harvesting would probably make use of much wider and longer strips.

Furthermore, this modelling could explain why *Eciton burchelli* is absent from Juan Gallegos Island, Panama (see section 1.1). This is one of a series of islands in Gatun Lake, along with Barro Colorado Island, which was formed by the flooding of valleys to construct the Panama Canal early in the twentieth century. Partridge et al. (1996) used a variant of the above model to predict which islands in Gatun Lake currently support populations of *E. burchelli*. The model's predictions were correct in all but one case, that of Juan Gallegos Island; it was predicted that *Eciton burchelli* ought to be present but the field data did not support this prediction. Parts of this island had previously been used for agriculture so that until recently its forests were fragmented. This modelling perhaps explains the absence of army ants.

The improved mean field model predicted that by decreasing  $M$  (i.e. the movement range) the abundance of *E. burchelli* declines. For example, a colony finding itself on a peninsula has less choice of patches to move to than a colony in the midst of the forest and hence should fare worse. This suggests that islands having a high edge to area ratio are not suitable reserves for *Eciton burchelli* army ants. This idea is expanded later in this chapter (section 2.3) by the use of fractal dimensions.

Possibly an important aspect of *Eciton burchelli* colony dynamics is queen death. The entire colony revolves around the queen and her egg-laying cycle; should she die it is probable that the entire colony will also cease to exist. The inclusion of queen death hence increases the turnover rate in a reserve. The easiest way to model this is to assume queens, and hence colonies, die with a constant probability during each cycle so that queen death is modelled by a Poisson process. Feeding this into the Markov Chain (2.3) leads to expressions of patch occupancy which are not suitable for analysis. However, queen death can be included through another approach, see chapter 3.

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## 2.2. AN ANALYTICAL MODEL OF HABITAT FRAGMENTATION

The mean field models make numerous assumptions which may be unreasonable. Firstly, every aspect of the biology has been regarded as random, be it colony movement or habitat destruction. The models cannot test for correlated habitat removal; an important issue when assessing potential conservation programmes. Secondly, real dispersal dynamics cannot be explicitly considered. For example, a colony of *Eciton burchelli* is unlikely to cross a large gap in the forest, but the mean field models, which in effect allow jumping, cannot consider this aspect; indeed Hassell et al. (1991) showed spatial structure is very important for certain insect populations.

## 2.3 A Computer Simulation of Habitat Fragmentation

As commented towards the end of the previous section, the mean field models have numerous problems associated with them, especially with their inability to explicitly deal with space. It is therefore necessary to investigate this aspect further by using a spatially realistic model of *Eciton burchelli*. In this section a computer simulation model is developed based around the mean field models of section 2.2, but the limited dispersal powers of the army ants are accounted for. Furthermore, queen death is easily included.

### 2.3.1 Description of Simulation Model

The simulation model is simply an extension of the above mean field models; a discrete-time stochastic cellular automata model (e.g. Caswell and Etter, 1993; Dytham, 1995b; Travis and Dytham, 1998). As before, a habitat patch is taken to be an area of rain forest roughly equal to the area raided by an *Eciton burchelli* colony during its statary phase. Time, recall, is related to the activity cycle of the ants, 1 time unit representing five weeks.

For the purpose of simulation, an arena consisting of 2500 patches (i.e. 50 cells  $\times$  50 cells, or an area of rain forest 9km  $\times$  9km) is considered. A number of patches are initially randomly, and later systematically, removed from the lattice, with reflecting boundary conditions (see below) imposed on these patches and on the edge of the

lattice. The system is then allowed to evolve subject to several transition rules:

1. Each colony chooses to move to any of the 24 patches at the edge of a  $7 \times 7$  square, the centre of which is the current position. See figure 2-2. This fixes the both the distance a colony moves (and is roughly equal to 530 metres, the direct overland distance between successive statary bivouacs (Willis, 1967; Franks and Fletcher, 1983)) as well as the initial direction. Hence a colony can migrate through any of the eight adjacent patches. Movement rules such as these have been used in numerous other models (e.g. Durrett and Levin, 1994; Dytham, 1995a; Travis and Dytham, 1998).
2. It moves continuously in that direction until it hits a removed patch or the edge of the lattice at which point it reflects, like a beam of light reflected by a mirror.
3. The colony stops moving when it has migrated the distance determined in step 1.

The reflecting boundary conditions imposed on the removed patches are consistent with observations made in Panama and elsewhere whereby *Eciton burchelli* colonies do not move for a prolonged time into areas that have no canopy cover (Willis and Oniki, 1978; Stouffer and Bierregaard, 1995, N. R. Franks, personal correspondence).

As before, a young patch is defined to be one that has been occupied in the last six time steps (because patch recovery time is 200 days (Franks, 1982a), a time step is 35 days and  $200/35 \approx 6$ ). Queen death is included here, unlike the analytical models of the previous section, and is assumed to occur via a Poisson process. Therefore, with probability  $1/(Q \times (365/35))$  the queen, and hence the entire colony, will die during the time step,  $Q$  being the queen's average lifespan in years (Partridge et al., 1996). For the simulation, the value  $Q = 6$  was chosen, biologically a not unreasonable figure (Franks, 1985).

In order to test the importance of patch shape and lattice design, two different lattice constructions were examined, one using square patches of side 180 metres and another using hexagonal patches of diameter 180 metres. (Compare the hexagonal

movement rules in figure 2-4 with the square movement rules in fig. 2-2.) All the remaining aspects of the models were identical.

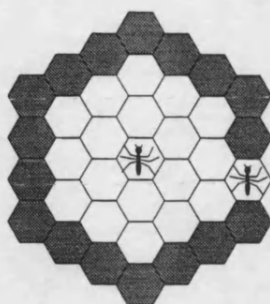


Figure 2-4: The hexagonal movement range. A colony on one patch will choose to move to any of the 18 patches of approximate distance 540 metres away, roughly the distance moved between successive statary bivouacs (Willis, 1967; Franks and Fletcher, 1983). Compare this movement rule with that in figure 2-2.

### 2.3.2 Random Patch Removal and Percolation Theory

A  $50 \times 50$  lattice was established as outlined above and a proportion of patches were then randomly removed ranging from zero to sixty percent in steps of four percent. A tenth of the remaining patches were then randomly occupied by colonies of size  $m = 5$ , the average colony size and density with no removed patches according to Britton et al. (1996) and section 2.2<sup>1</sup>. The system was then allowed to run for a sufficiently long time until a steady state was reached (typically 500 time steps – i.e. fifty years) and data on the last 300 time steps was recorded – this corresponding to the quasi-equilibrium state. Each such simulation was repeated twenty times.

#### Percolation Theory

Percolation theory (see, for example, Kesten, 1982; Stauffer, 1985) is a well developed branch of mathematics dealing with the connectivity of lattices and so is particularly useful here. For square lattices (with nearest and next-nearest neighbour movement) and hexagonal lattices (with nearest neighbour movement only), percolation theory

<sup>1</sup>Various other initial conditions were tested with no difference to results.

predicts the existence of a critical proportion of patches  $p_c$  which can be removed before the (infinite) lattice fragments. Note that here the word 'fragment' is used in a mathematical as opposed to a biological sense, and refers to the event where the expected cluster size (i.e. the number of connected patches) changes from being infinite to being finite.

For square lattices with the neighbourhood being the eight adjacent cells, the critical percolation threshold has been approximated from computer simulations to be  $p_c = 0.5928$ . As a demonstration and a useful exercise for later on, figure 2-5 shows the largest cluster size on a  $50 \times 50$  lattice as a number of squares are randomly removed which is determined by an exhaustive search. Note that when less than 60% of the patches have been removed the lattice basically consists of a large single connected cluster with possibly a few isolated patches. When more than 60% are removed, all that remains are numerous small unconnected clusters.

For hexagonal lattices, the situation is similar, only the critical percolation value has been proven to be  $p_c = 0.5$  (see, for example, Kesten, 1982).

### Mean Number of Colonies

When habitat patches are removed from both the square and hexagonal lattices, the number of colonies the reserve is able to support declines (figs. 2-6(a) & 2-7). What is surprising, however, is that even when there exists a large (possibly infinite!) connected cluster, *Eciton burchelli* persistence could be impossible.

As the proportion of removed patches on the square lattice approaches 0.45, the number of colonies approaches zero, i.e. extinction. What is surprising here is that extinction occurs well before the lattice is broken up into clusters (fig. 2-5). This phenomenon occurs because, even though it is not impossible for a colony to get from one site in the cluster to any other, it may be very difficult (see figure 2-8). Hence a colony will predominantly occupy only a region of the cluster and not necessarily the whole cluster. So a habitat which appears to be both sufficiently large and continuous enough to support a population of *Eciton burchelli* may be unable to do so. One way

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### 2.3. A COMPUTER SIMULATION OF HABITAT FRAGMENTATION

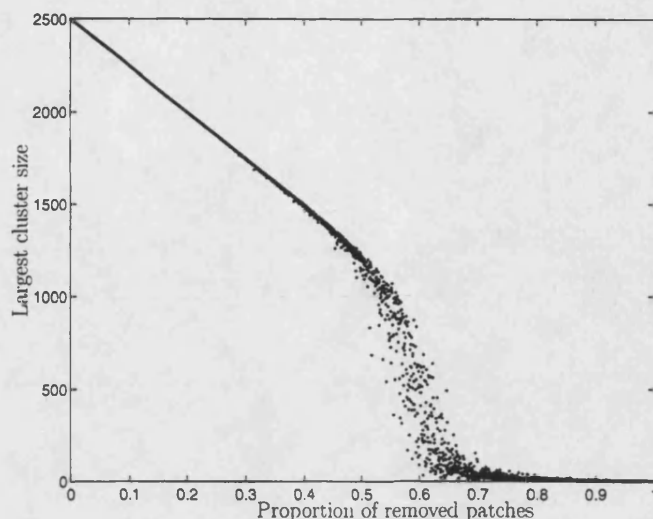


Figure 2-5: The size of the largest cluster is plotted as a function of the proportion of patches removed for a  $50 \times 50$  square lattice. Initially one patch is randomly removed from the  $50 \times 50$  lattice and the largest cluster size is calculated. Then two patches are randomly removed from the  $50 \times 50$  lattice and so on until 2500 patches are randomly removed. The whole process is repeated five times, making the total number of lattices considered  $5 \times 50 \times 50 = 12500$ . Patches are neighbours in the sense of nearest and next-nearest cells. Notice that when less than 60% of the patches are removed the lattice consists of just one connected cluster with possibly a few isolated patches. When more than 60% are removed, we obtain many small unconnected clusters. This graph suggests the critical percolation value occurs when  $p_c \approx 0.6$ .

of emphasising this is to remove from the  $50 \times 50$  lattice 0.45 of the habitat but leave the remaining habitat as a large single square. This 'remnant' will support about 100 colonies almost indefinitely (Britton et al., 1996; Partridge et al., 1996).

Thus, from this perspective, it would be preferable to remove habitat in larger clumps, rather than the square patches of side 180m considered here. This shall be tested later in section 2.3.3.

### Mean Number of Old Patches

The mean number of old or recovered patches undergoes a peculiar change as habitat patches are randomly removed on both the square and hexagonal lattices (fig. 2-9). As blocks of habitat are removed, the number of old patches actually rises. Such

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## 2.3. A COMPUTER SIMULATION OF HABITAT FRAGMENTATION

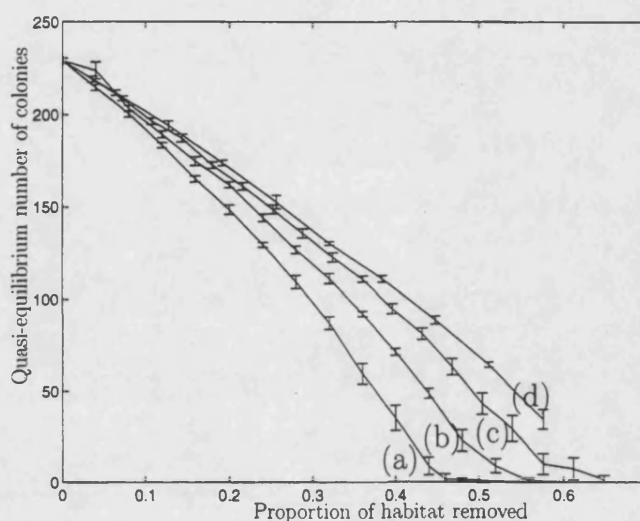


Figure 2-6: A proportion of habitat is randomly destroyed starting from 0 and changing in small increments (typically 0.04). One tenth of the remaining habitat is then populated by colonies and the simulation is allowed to run for 500 cycles with only the last 300 iterations begin recorded; allowing a quasi-steady state to be reached. The habitat is removed in various ways as documented in the text; (a)  $1 \times 1$  blocks, (b)  $2 \times 2$  non-overlapping blocks, (c)  $3 \times 3$  non-overlapping blocks, and (d)  $4 \times 4$  non-overlapping blocks. Each simulation is repeated twenty times and the mean with 95 % confidence intervals is shown. In (d) it becomes impossible to remove a  $4 \times 4$  block of habitat once a certain amount of habitat is removed, simply because the habitat is of such a complex shape.

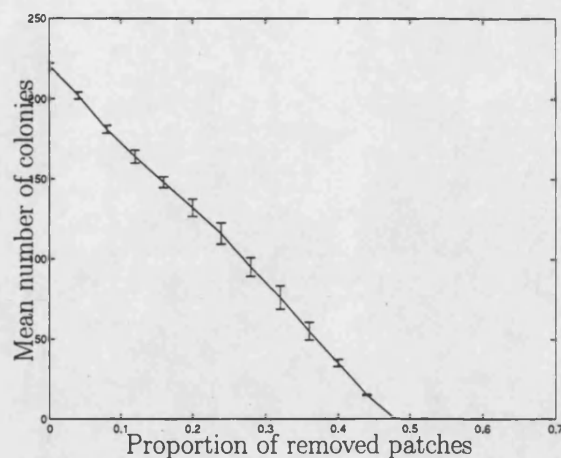


Figure 2-7: The average number of colonies as a function of the proportion of removed patches with 95% confidence intervals. Twenty simulations were conducted in each case for differing amounts of randomly removed habitat from a  $50 \times 50$  hexagonal lattice. Notice there is a transition from persistence to extinction when the proportion of removed habitat reaches 0.48. In fact, this amount is independent of reserve size.

bizarre findings are consistent with other cellular automata models considering habitat removal (e.g. Dytham, 1995a).

This surprising result can be explained by the same argument used in the unexpected level of army ant extinction. As patches are randomly removed, small clusters unable to support a single colony are formed, consisting of old patches. Also, the large cluster, as will almost certainly exist (fig. 2-5), will include 'just-connected' pockets – a small collection of patches unable to support a single colony but are accessible from the main body of the cluster (see fig. 2-8). Since these pockets are rarely entered, they nearly always consist of old patches. As the lattice has further patches removed, these 'just-connected' pockets increase in abundance, until they eventually dominate the lattice and army ant persistence is impossible.

### 2.3.3 Correlated Patch Removal

It was argued above that by removing the habitat in larger blocks, as opposed to single patches, the abundance of *Eciton burchelli* should be improved. This is tested in the square-patch simulation model by repeating the simulations but with four different



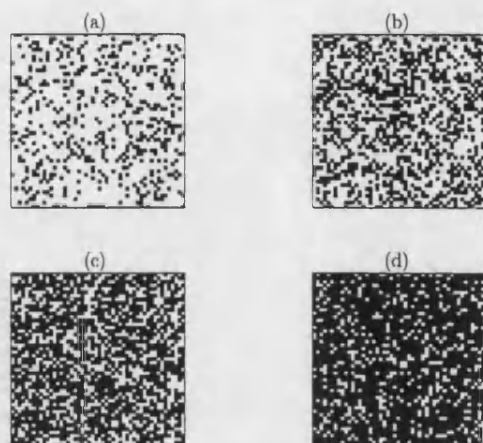


Figure 2-8: The typical structure of the square lattice with (a) 20%, (b) 40%, (c) 60% and (d) 80% of the habitat randomly removed. The black patches denote removed habitat, while the white squares represent existing habitat. Notice that in (a) the habitat is clearly connected and in (d) it is clearly unconnected. The situation in (b) and (c) is not quite so clear (although in fact (b) is connected in the sense of nearest and next-nearest neighbours).

habitat removal strategies:

- (i) Random removal of patches as earlier
- (ii) Removal in non-overlapping blocks of  $2 \times 2$
- (iii) Removal in non-overlapping blocks of  $3 \times 3$
- (iv) Removal in non-overlapping blocks of  $4 \times 4$ .

Intuitively, by removing habitat in larger blocks, the degree of fragmentation should be reduced. Figure 2-10 provides an illustration of this. Since the degree of fragmentation is reduced, the abundance of the army ants should then improve – figure 2-6 shows this is precisely the case.

### 2.3.4 Habitat Removal and Fractal Dimensions

Above it was seen that both the area of a reserve and some measure of connectedness greatly influenced the equilibrium number of colonies. Here we shall quantify this by

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## 2.3. A COMPUTER SIMULATION OF HABITAT FRAGMENTATION

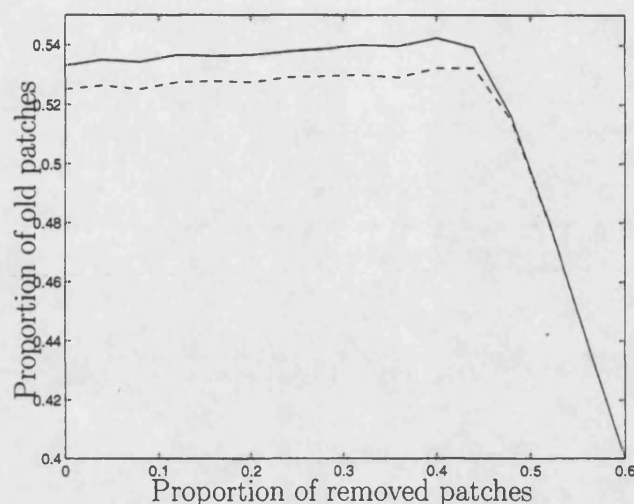


Figure 2-9: The mean proportion of old patches as a function of the proportion of removed patches for the square lattice (solid line) and the hexagonal lattice (dotted line). Notice at first when little habitat is removed, roughly half of the reserve consists of old patches, agreeing with empirical studies (e.g. Franks, 1982a). As more habitat is removed, the number of old patches actually increases until army ant persistence becomes impossible so that every patch becomes an old patch.

using fractal dimensions. Fractal dimensions have been used in other theoretical studies of reserve design (see, for example O'Neill et al., 1992) with a range of conclusions.

Benoit Mandelbrot in his 1977 book “Fractals: Form, Chance, and Dimension” explained the origin of the word *fractal*: it derives from the Latin adjective *fractus*, having the same root as *fraction* and *fragment*, and means irregular or fragmented. It seems then very natural and certainly appropriate to apply the theory of fractal dimensions to the problem of habitat fragmentation. The fractal dimension of a shape is a measure of how elongated it is, or said differently, how well it fills the domain in which it lies. We shall obviously be concerned with the domain  $\mathbb{R}^2$ . The fractal dimension of a square in  $\mathbb{R}^2$  is 2, whilst a shape resembling a straight line will have a fractal dimension of roughly 1. The hypothesis from the previous section can now be stated more precisely as

(H1) “the larger the reserve and the greater its fractal dimension, the more army ant colonies it should support.”

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### 2.3. A COMPUTER SIMULATION OF HABITAT FRAGMENTATION

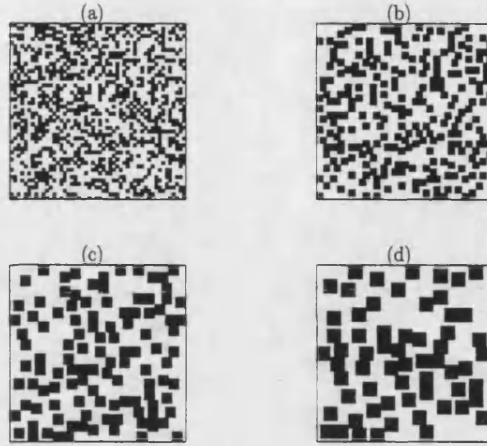


Figure 2-10: The effect of removing 40% of the habitat from a  $50 \times 50$  square lattice. The black patches denote the removed habitat; the white patches represent forested areas. (a) The patches are removed randomly. (b) The patches are removed randomly but in non-overlapping blocks of four patches (i.e.  $2 \times 2$ ). (c) The habitat is removed in non-overlapping blocks of  $3 \times 3$  and (d) habitat removal in blocks of  $4 \times 4$ . Notice that the degree of fragmentation in (d) is much less than that in (a).

For fragmented lattices, such as those in figs 2-8 & 2-10, the fractal dimension is best approximated by the box-counting method (Barnsley, 1988; Feder, 1988; Peitgen et al., 1992). The lattice is rescaled by defining the unit length to be 180 metres – the length of a patch side. The box-counting method now requires the habitable patches in the lattice to be covered by the minimum number of square boxes  $N(R)$  of side  $R \in \mathbb{R}$ . The values of  $N(R)$  are approximated for a series of  $R$  by a computer program. The relationship between the fractal dimension of the habitable reserve  $D$ , the box side  $R$  and the minimum number of boxes required to span the habitable lattice is then (Barnsley, 1988; Feder, 1988)

$$N(R) = aR^{-D} \quad (2.19)$$

so that  $D$  can be estimated by plotting a graph of  $\log R$  against  $\log N$  and calculating the gradient of the line of best fit.

A series of square lattices ranging in size from  $10 \times 10$  going up in steps of 10 to  $60 \times 60$  were constructed. Patches were then removed from these lattices in the four different

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### 2.3. A COMPUTER SIMULATION OF HABITAT FRAGMENTATION

ways as stated in section 2.3.3. The proportion removed from each lattice ranged from 0 to 60%, incrementing in steps of 5%. The fractal dimension of the resulting habitable reserve was calculated along with the quasi-equilibrium number of colonies as explained in section 2.3.1, and was repeated eight times for each patch removal scenario (thus the total number of lattices considered was  $6 \times 4 \times 13 \times 8 = 2496$ ). A collection of 'bins' were then constructed, corresponding to lattices having similar area and similar fractal dimensions, and the average number of colonies for each bin was calculated. Figure 2-11 shows how the the quasi-equilibrium number of *Eciton burchelli* colonies depends on reserve area and fractal dimension. Notice especially, habitats of small area or low fractal dimension make poor reserves, while those of larger areas and high fractal dimension makes good reserves.

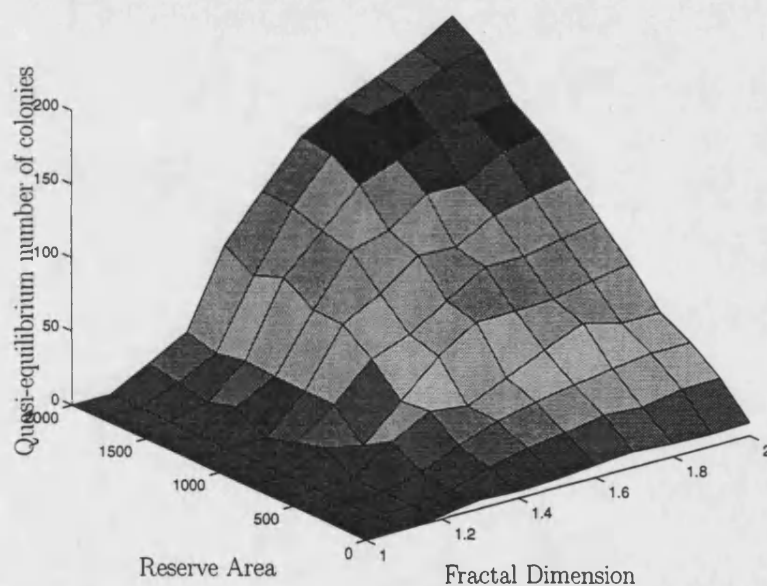


Figure 2-11: Approximately 2500 lattices are examined which have had various amounts of habitat removed in various fashions as documented in the text. The fractal dimension of each lattice is determined (via the box-counting method) along with the lattice's area and quasi-equilibrium number of colonies. The lattices are grouped into classes of similar area and fractal dimension and the average number of colonies is plotted for each class. It is clear that small reserves cannot support any colonies and neither can lattices with a low fractal dimension.

This result agrees exactly with hypothesis (H1). *Eciton burchelli* army ants are more

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### 2.3. A COMPUTER SIMULATION OF HABITAT FRAGMENTATION

of an internal species than an edge specialist by their avoidance of open areas. Their best reserves will thus have a low edge:area ratio, i.e. will have a high fractal dimension. Of particular interest is the region in figure 2-11 where persistence is impossible. We cannot, using the current mathematical model, investigate this more fully, as we are limited in removing square blocks of side 180 metres.

The fractal dimension work suggests an extension of the classic species-area theory (MacArthur and Wilson, 1967). Recall, species-area theory states there is a relationship between the size of a reserve,  $A$ , and the expected number of species to be found in it,  $S$ , given by

$$S = cA^z \quad (2.20)$$

where  $c$  and  $z$  are some parameters related to the type of habitat considered, the taxons and the population density. Hamilton-Wright (1983) furthered this idea to form the species-energy theory – a natural extension where area is replaced by energy. Typically, but not always as he demonstrates, there is a linear relationship between reserve area and its energy. Our work above suggests a further improvement, namely area (or energy) should be replaced with *usable* area (or *usable* energy) since clearly area alone is not enough to predict species abundance. It is not my intention here to develop this idea any further.

### 2.3.5 Discussion of Simulation Model: Implications for Conservation

The importance of these results can be seen when one considers so-called sustainable harvesting strategies, which involve felling long strips of woodland (Hartshorn, 1989, 1995) so that a large forest is broken up into strips. These forested strips are internally fragmented by streams, access roads, tree-fall gaps, etc... so that the actual cluster size may be a great deal smaller than one might first suspect. The simulations predict that if the clusters are too small, or too inaccessible, then at the very least, the army ant *Eciton burchelli* will become locally extinct.

The results suggest a better sustainable forest harvesting strategy is to remove

reasonably large square-like clumps, leaving the remaining habitat with a large a fractal dimension as possible. Of course this is a very one-sided view; it is going to take less time for the forest to recover if felling is in the form many strips than a few larger square clumps. However, the value of faster recovery would be diminished because it would involve a cost: species reduction.

An important issue raised by this modelling relates to the optimal design of nature reserves (Game, 1980; Simberloff, 1988). We have seen from figure 2-11 that for *Eciton burchelli* army ants, the optimal reserve shape is square or circular-like – but certainly not long and narrow. This is typical for internal specialists, but of course, edge specialists have different preferences. Clearly, reserve design is an issue of balance within the ecosystem for which it is intended, and for *Eciton burchelli*, is beyond the scope of this thesis.

As discussed above, long-narrow reserves, having a low fractal dimension, are useless for *Eciton burchelli*. A colony finding itself in such a reserve typically wanders back and forth over a small region, depleting its food supply without giving it a chance to recover. A habitat corridor, being a linear strip of habitat, clearly has a fractal dimension close to 1 and thus will not only be a very poor reserve, but could also act as a demographic sink. This important possibility is examined in detail in chapter 4.

A number of authors have examined the effect of habitat removal on population persistence (e.g. Dytham, 1995a; With and Crist, 1995; Bascompte and Solé, 1996). For example, Dytham (1995a) examined the effect of habitat removal on two interacting populations but did not interpret his results using percolation theory. He investigated how two species in competition fared in a fragmented environment where one was a superior disperser and the other a superior competitor. His neighbourhood rules were similar to the square-patch simulation, namely direct movement into the eight adjacent cells. The dominant competitor went extinct while the habitat was still connected; the better disperser persisted until the percolation critical value was achieved, at which point there was a sudden shift in the abundance of this species. These results are entirely to be expected with the use of percolation theory (see also With and Crist,

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### 2.3. A COMPUTER SIMULATION OF HABITAT FRAGMENTATION

1995; Bascompte and Solé, 1996).

Of course, the equilibrium number of colonies does not tell the whole story. Almost surely any population will eventually become extinct (MacArthur and Wilson, 1967; Levins, 1970). However, the expected time to extinction depends very strongly on the quasi-equilibrium number of colonies (Partridge et al., 1996, see also chapter 3) and this emphasises the importance of not allowing the equilibrium number of colonies to fall too low.

The model's predictions may be tested by appealing to the methods and results of chapter 3. In that chapter, expected extinction times and distributions are obtained for reserves of varying quality. Hence, given forest fragments which have been isolated from other remnants for a known time, the probability that a reserve currently supports populations of *Eciton burchelli* can be estimated. By finding sufficiently many fragments of varying sizes and shapes, presence or absence of the army ants can be compared between the model and the field data.

It is concluded that any future strategy for tropical rain forest management is going to take a great many issues on board: to look not only at short-term solutions but more long term effects as well. Conservationists must examine the trade-off between quicker forest recovery and an increased extinction risk of certain species.

## 2.4 Summary

In this chapter I have described the current scale of deforestation and how mathematical modelling might aid in limiting its effects. Some general analytical models were stated as well as more involved simulation models; the conclusions are varied but all predict extinctions under sufficient habitat removal.

An analytical model of Britton et al. (1996) for *Eciton burchelli* army ants was extended to cope with habitat removal. Initially a size-structured mean field model was considered, where colony dispersal was essentially unbounded. It was observed that, like numerous other models, there existed a critical proportion of habitat which could be permanently degraded before the species were forced extinct (in this instance

the critical amount was  $1/2$ ). An improved mean field model was then considered, where dispersal was bounded, and, like the mean field model, there existed critical amounts of habitat that could be degraded before extinction. The improved mean field model predicted extinctions would be caused by lower amounts of habitat removal than the mean field model. This suggested spatial effects were important.

A computer simulation was then developed in order to explore the importance of spatial effects on army ant extinctions. Using percolation theory, it was seen that even infinitely-large habitats may not support populations of *Eciton burchelli*, thus making area alone an exceptionally poor measure of a reserve. It was also observed that the removal of a single large patch of rain forest was preferable to removing several smaller patches, but how this effects forest recovery is unclear. Finally it was seen that it is possible to quantitatively describe how good a reserve is by considering its area in conjunction with its fractal dimension. This has important implications for habitat corridors which are the topic of chapter 4.



## Chapter 3

# Catastrophes

The fate of any species ever to have existed, or which ever will exist, is ultimately extinction. Whether extinction occurs over vast time scales or very rapidly depends on numerous factors ranging from small shifts in the micro-environment to massive climatic changes. The goal of conservation is to reduce the risk of extinction; this requires a measure of species persistence. In this chapter we use the expected time to extinction as such a measure. By using this important and universal statistic, conservation schemes around the world can be compared and, more importantly for funding bodies, be given priority.

In section 3.1 the expected extinction time is considered as a measure of species persistence and it is stressed how this measure ought and ought not to be interpreted. Numerous models are mentioned capable of calculating this statistic, and it is seen that only a very few include catastrophes – events of mass population decline – as might be caused by sudden climatic change. It is shown in this section, through real examples, that catastrophes have an important rôle in determining persistence. In section 3.2, using the model of chapter 2, analytical expressions for the birth and death rates of *Eciton burchelli* army ant colonies are derived, from which population distributions and expected extinction times are obtained, the methods being mainly based around Markov Chains. The influence of catastrophes on persistence times is then examined over a range of catastrophe types and reserve sizes. The Markov Chain

approach, whilst effective, is expensive, requiring the solution of large systems of linear equations. To this end, in section 3.3 simple analytical approximations are derived for the expected time to extinction and under most conditions are in good agreement with the MC model, the exception being very small reserves supporting few individuals at the quasi-equilibrium; such situations are, however, very suited to the MC model.

### 3.1 Catastrophes: Examples and Models

Given the limited funding available for most conservation programmes, it is crucial such schemes target the appropriate species in their attempts to save the natural world; a measure of a species persistence is paramount to this. There are a variety of such measures in the literature, but probably the most useful and universal is the expected time to extinction. It serves as a useful statistic of the population's current state of persistence, but is often misinterpreted since no account is made by this measure for population genetics. For example, if a population has an expected extinction time of  $T$  years, it should not be interpreted that the population will persist on average for  $T$  years since genetic effects may alter important characteristics in the population dynamics, changing the expected extinction time; it should be used as an assessment of risk in the short to medium term. It is clearly those species having the shortest expected time to extinction for whom conservation efforts must take priority. Also, it is often desirable to obtain information on the distribution of persistence times so that, for example, reserves may be constructed having a 95% chance of lasting for 100 years.

Most extinctions have two underlying causes; a deterministic drift and a stochastic process (Simberloff, 1988; Harvey and May, 1997; Ludwig, 1999). In large populations, demographic and environmental stochasticity have little influence on population dynamics; their effects are averaged out over the population. However, should the population be reduced, for example by a deterministic process, e.g. over-harvesting, both demographic and environmental stochasticity become increasingly important to the fate of the population. A classic example in the literature is provided by the Heath hen (Simberloff, 1988) whose numbers were reduced by over-harvesting but finally forced

extinct by a combination of disease, climatic events, fire and extreme predation.

The tropical rain forests, and *Eciton burchelli* army ants in particular, are subject to numerous catastrophes. For example, El-Niño events are becoming more common in recent years (Wuethrich, 1995) and their effects are both numerous and wide-ranging (Condit et al., 1996a,b). Increasing human exploitation of the rain forests both reduces habitat quality (a deterministic process) and leads to increased risks of fires and disease transmission (stochastic events). Disasters such as these may have a tremendous influence on the expected time to extinction and are clearly worthy of thorough investigation.

### 3.1.1 Modelling Disasters and Times to Extinction

The expected time to extinction, singularly the most important statistic for the design of conservation programmes, cannot easily be obtained from field experiments – it must be estimated through careful mathematical modelling. There are, however, surprisingly few models including catastrophes which are capable of calculating this crucial figure; most tending to be discrete-based simply because those populations likely to go extinct are small and therefore individual-based models are most appropriate.

MacArthur and Wilson (1967) were the first people to introduce formally, at least in a mathematical sense, the concept of the expected time to extinction. Their model was simple, considering a single island with constant birth and death rates up to some population ceiling. A Markov Chain was formed whose states corresponded to the number of individuals on the island and the expected time to reach state 0, i.e. extinction, is easily found from the classic methods associated with finite state Markov Chains (e.g. Karlin and Taylor, 1981).

Nisbet and Gurney (1982) provided a simple method of calculating the expected time to extinction for a metapopulation. Their method involved relating colonisation and extinction in a metapopulation to birth and death in stochastic population dynamics. A stochastic differential equation is derived, based around Levins' model (2.1), and by examining fluctuations in patch occupancy a crude estimate of the expected time

to extinction is given by

$$\tau_e \approx \tau_L \exp \left\{ \frac{Q^2}{2(M - Q)} \right\}$$

where  $M$  is the number of patches in the metapopulation,  $Q$  the number of occupied patches at the quasi-steady state and  $\tau_L$  the average lifetime of a patch. Notice this method fails to include population levels on each patch, and therefore the rescue effect of Brown and Kodric-Brown (1977) (as mentioned on page 20). It is also a very poor estimate when  $Q$  is small, which are precisely those populations most at risk from extinction.

Mangel and Tier (1993) (see also Mangel and Tier, 1994) introduced a simple method, again based around Markov Chains, to calculate expected extinction times. Their method, which is used in section 3.2.3, allows species to have incredibly complicated non-linear dynamics, includes catastrophes and simply reduces to the solution of a large (though often sparse) linear system of equations. They also give examples of catastrophes having tremendous effects on the expected time to extinction.

The above examples used discrete state space models, because firstly they were appropriate to the problem, and secondly were relatively simple. It is important to realise that the expected persistence times for large populations must also be calculated, since under disasters, even large populations may be quickly forced extinct – the above methods are too expensive and impractical for such systems. Several authors have tried to rectify this. Lande (1993) modelled a population by a diffusion process. He assumed the population grew exponentially up to a fixed ceiling and was subjected to catastrophes occurring via a Poisson process at each time removing a fixed proportion of the population. A first order solution of the diffusion process was obtained giving approximate expected extinction times. Hastings (1995) introduced a general model to calculate extinction times for large populations subject to sudden population jumps (i.e. catastrophes) which involved solving a complicated partial-integrodifferential equation. Even the simple assumptions of his model gave rise to complicated, and mostly intractable, analytical expressions for the extinction times. More recently, Ludwig

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### 3.1. CATASTROPHES: EXAMPLES AND MODELS

(1996) attempted to model population growth also by a diffusion equation, his results differed substantially from other more basic models suggesting the diffusion approach is not a good approximation. The estimation of extinction for large populations is an open problem whose solution should be given priority; a novel solution is presented here in section 3.3.

## 3.2 Birth and Death Rates, Population Distributions and Times to Extinction

Britton et al. (1999) introduced a method of estimating the expected time to extinction for *Eciton burchelli* army ants without including catastrophes. Their method involved an estimate of the colony birth and death rates from the model of section 2.2; similar expressions are derived in section 3.2.1 but via conditional probability. From knowledge of the birth and death rates, a probability distribution for population numbers can be constructed, see section 3.2.2. Using this distribution, the impacts of catastrophes on population structure is easily examined. Then in section 3.2.3, using the analytical expressions for colony birth and death rates, the expected extinction time is obtained.

### 3.2.1 Birth and Death Rates

An event in the lifetime of a colony is defined here to be either a colony division (i.e. a birth) or a colony death, and the event rate is simply the reciprocal of the expected time to an event. Thus if the event rate is  $r$  and the probability the event is a birth is  $p$ , the birth rate is given by  $pr$  and the death rate by  $(1 - p)r$ . In this section we first calculate the expected event rate and then consider the probabilities of the various types of events. Ultimately combining these expressions yields the birth and death rates.

Consider an army ant colony moving from one patch to another, as in chapter 2, and so changing size at every time step, either increasing or decreasing one population unit depending on the quality of the patch it lands on (recall, for *Eciton burchelli* one

population unit is about 60 000 worker ants). If the colony decays to size 0 it is dead while if it reaches size  $2m$  ( $m \in \mathbb{N}$ ) it splits into two separate colonies, each of size  $m$ . This can be modelled as a random walk on the integers between 0 and  $2m$ .

The probability a colony grows in a time step is precisely the chance it lands on an old patch – one with plenty of insect prey – which, to a first approximation (i.e. the mean field) is just the proportion of old patches on the island. (Recall, a patch is old if it has not been raided in the last  $n$  time steps.) Assuming the number of colonies in a reserve does not change dramatically over  $n$  time steps (which is reasonable since most of the time the system will be near the quasi-equilibria), we approximate  $p$ , the probability of landing on an old patch, to be

$$p = \left(1 - \frac{N}{K}\right)^n \quad (3.1)$$

where the island has  $N$  of its  $K$  patches currently occupied. Write  $q = 1 - p$  to denote the probability of raiding a young patch so that in the random walk approximation, with probability  $p$  the system goes up one step whilst with probability  $q$  it goes down one step.

We now consider queen death as an additional cause of colony death. It is postulated (Partridge et al., 1996, see also chapter 2) that in the event of queen death, the entire colony will most likely die also. Suppose that with fixed probability  $\delta$ , the queen, and hence the entire colony, will die during any time step; queen death is thus modelled as a Poisson process occurring at rate  $\delta$ .

Define  $X_k$  to be a random variable of the waiting time for a colony of size  $k$  to hit either 0 or  $2m$  (i.e. either a colony division or a colony death) and let  $T_k = \mathbb{E}[X_k]$  denote the expected waiting time. Then conditional expectation says

$$\mathbb{E}[X_k] = \mathbb{E}[\mathbb{E}[X_k|Y]] \quad k = 1, \dots, 2m - 1. \quad (3.2)$$

Suppose  $Y$  is the fortune of the queen, i.e. whether she lives or dies during the current

time step. Then equation (3.2) is simply

$$\begin{aligned}\mathbb{E}[X_k] &= \mathbb{E}[X_k | \text{queen dies in current cycle}] \mathbb{P}(\text{queen dies in current cycle}) \\ &+ \mathbb{E}[X_k | \text{queen survives current cycle}] \mathbb{P}(\text{queen survives current cycle}).\end{aligned}$$

Clearly, the first term on the right hand side is zero since we know the colony dies, so we arrive at

$$T_k = \mathbb{E}[X_k | \text{queen survives current activity cycle}] (1 - \delta). \quad (3.3)$$

Now define  $\chi_k = \mathbb{E}[X_k | \text{queen survives this time step}]$  so equation (3.3) may be written as

$$T_k = \chi_k (1 - \delta) \quad k = 1, \dots, 2m - 1. \quad (3.4)$$

Consider  $\chi_k$  as a random walk currently at state  $k$ . Since it is known the queen survives this cycle, at the next time step the random walk will be at state  $k + 1$  with probability  $p$  or at state  $k - 1$  with probability  $q$ . Hence  $\chi_k$  will satisfy

$$\chi_k = 1 + pT_{k+1} + qT_{k-1},$$

the '1' arising since the colony survives this one cycle. Combining this with relation (3.4) shows the  $\chi_k$ 's satisfy

$$\chi_k = 1 + p(1 - \delta)\chi_{k+1} + q(1 - \delta)\chi_{k-1} \quad k = 1, \dots, 2m - 1. \quad (3.5)$$

To solve this system, boundary conditions must be specified at the end points  $k = 0$  and  $k = 2m$ . Clearly, given the definition of  $\chi_k$  (the expected time to an event, which is either a birth or death), the boundary conditions are

$$\chi_0 = \chi_{2m} = 0. \quad (3.6)$$

Thus (3.5) and (3.6) form a system of  $(2m - 1)$  linear equations which are easily solved on a computer. The expected waiting time to an event for a single colony (either colony division or colony death) is then  $T_m = \chi_m(1 - \delta)$  since the initial colony size is  $m$ . Thus the event rate per colony is

$$\tau = \frac{1}{T_m}. \quad (3.7)$$

To obtain the birth and death rates we require the probability the random walk hits  $2m$  before it hits 0 and vice-versa. To this end, define

$$Y_k := \mathbb{P}_k(\text{Hit } 2m \text{ before } 0 | \text{start at } k).$$

Then obviously

$$\begin{aligned} Y_k &= \mathbb{P}_k(\text{Hit } 2m \text{ before } 0 \text{ AND queen survives cycle}) \\ &\quad + \mathbb{P}_k(\text{Hit } 2m \text{ before } 0 \text{ AND queen dies in cycle}) \\ &= \mathbb{P}_k(\text{Hit } 2m \text{ before } 0 \text{ AND queen survives cycle}) \\ &= \mathbb{P}_k(\text{Hit } 2m \text{ before } 0 | \text{queen survives cycle}) \times \mathbb{P}_k(\text{queen survives cycle}) \end{aligned}$$

where we have used Bayes formula for conditional probability

$$\mathbb{P}(A|B) = \frac{\mathbb{P}(A \cap B)}{\mathbb{P}(B)}.$$

Let us now define  $\xi_k = \mathbb{P}(\text{Hit } 2m \text{ before } 0 | \text{queen survives cycle})$  so that  $Y_k$  satisfies

$$Y_k = \xi_k(1 - \delta). \quad (3.8)$$

Now consider the  $\xi_k$ 's as a random walk. Since the queen does not die during the current time step, at the next time step the random walk will either be at level  $k + 1$



with probability  $p$  or at level  $k - 1$  with probability  $q$ . Hence the  $\xi_k$ 's will satisfy

$$\xi_k = pY_{k+1} + qY_{k-1}$$

which upon applying (3.8) reduces to

$$\xi_k = p(1 - \delta)\xi_{k+1} + q(1 - \delta)\xi_{k-1} \quad k = 1, \dots, 2m - 1. \quad (3.9)$$

We now require the appropriate boundary conditions which, from the definition of  $\xi_k$ , are seen to be

$$\xi_0 = 0, \quad \xi_{2m} = 1. \quad (3.10)$$

The system (3.9–3.10) forms yet another linear system of  $2m - 1$  equations which can easily be solved on a computer<sup>1</sup>. Thus the probability a newly formed colony splits before dying is  $Y_m = \xi_m(1 - \delta)$  and the probability it dies first is simply  $1 - Y_m$ . From equation (3.7) the *per colony* birth rate is then

$$\frac{\mathbb{P}(\text{splits before dying})}{\mathbb{E}[\text{Time to birth or death}]} = \frac{Y_m}{T_m}$$

and the *per colony* death rate is defined similarly. For the metapopulation as a whole, the birth and death rates are the number of colonies on the island multiplied by the per colony rates. Hence the birth rate of the metapopulation is

$$B(N) = \frac{Y_m}{T_m} N \quad (3.11)$$

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<sup>1</sup>Notice that equation (3.5) with boundary conditions (3.6) can be written in the form  $A\mathbf{x} = \mathbf{b}$  where  $\mathbf{x}$  is the column vector of the  $\chi_k$ 's. Thus the  $\chi_k$ 's can be found from the formula  $\mathbf{x} = A^{-1}\mathbf{b}$  where  $A^{-1}$  is the matrix inverse of  $A$ . Now notice the system (3.9–3.10) can also be written in the same form  $A\mathbf{x}' = \mathbf{b}'$  with  $A$  being the same matrix in both cases. Since we have already calculated  $A^{-1}$ , this second system is easily computed. In fact, it is often unnecessary to calculate  $A^{-1}$ ; schemes such as Gaussian elimination provide much more efficient methods of solving linear systems – this is the approach used here.

and the metapopulation death rate is

$$D(N) = \frac{1 - Y_m}{T_m} N. \quad (3.12)$$

Figure 3-1 shows the birth and death rates for *Eciton burchelli* on Barro Colorado Island, Panama. The metapopulation is at its quasi-equilibrium precisely when the birth and death rates are equal. The average number of colonies on BCI predicted by this model which, unlike the analytical models of chapter 2 includes queen death, is in very good agreement with the data (Franks and Fletcher, 1983).

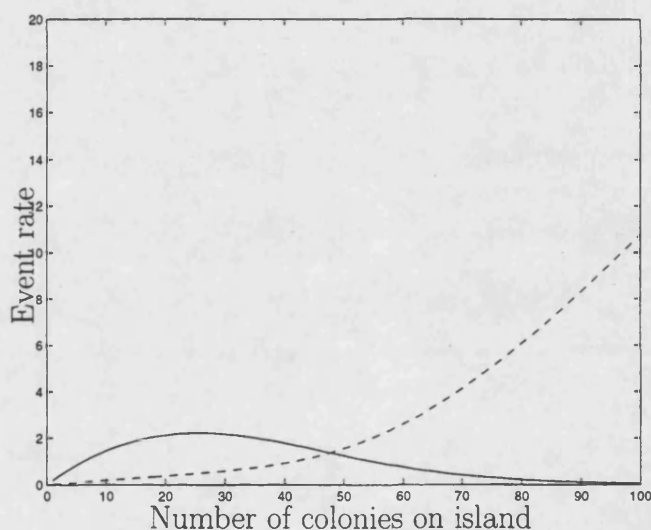


Figure 3-1: The birth (solid line) and death (dashed line) rates are plotted for Barro Colorado Island, Panama ( $K = 500, n = 6, m = 5, \delta = 1/60$ ). The equilibrium number of colonies on the island is about 48, which agrees very well with the field data (Franks and Bossert, 1983).

### 3.2.2 Conditional Population Distributions

With knowledge of the birth and death rates, as has been determined above, one can construct probability distributions for the population numbers in a reserve (see, for example, Gyllenberg and Silvestrov, 1994) – an easily testable prediction. Nisbet and Gurney (1982) present a method of calculating population distributions for general stochastic birth and death processes without catastrophes. Their algorithm, which is

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### 3.2. BIRTH AND DEATH RATES, POPULATION DISTRIBUTIONS AND TIMES TO EXTINCTION

used in section 3.3.2, is repeated below for convenience.

Suppose a population of  $i$  individuals has birth rate  $B(i)$  and death rate  $D(i)$ , and define

$$P(i) := \mathbb{P}(\text{population is } i \text{ individuals} | \text{population is not yet extinct}).$$

Thus, by comparing the flow between populations of size  $i$  and  $i + 1$ ,

$$B(i)P(i) = D(i + 1)P(i + 1) \quad \forall i \in \mathbb{N} \quad (3.13)$$

and then the  $P(i)$ 's may be obtained by the following algorithm:

- (i) Choose  $P(1)$  at random
- (ii) For all  $i > 1$ , calculate  $P(i + 1) = \frac{B(i)}{D(i+1)}P(i)$  until  $B(i)$  is sufficiently small
- (iii) If  $P(1)$  is significantly different from  $\frac{P(1)}{\sum P}$ , set  $P(1)$  to be  $\frac{P(1)}{\sum P}$  and repeat step (ii).

When a population is subject to a catastrophe, the population distribution will change. If the catastrophes are small and rare, this difference is most likely negligible, but should the catastrophe rate be sufficiently high the difference may be noticeable. The above algorithm cannot be adapted in this instance, as explained later in section 3.3.3, so a more basic approach is desirable.

Assume a population consisting of  $N$  individuals has birth rate  $B(N)$ , death rate  $D(N)$  and a population ceiling of  $K$  (thus  $B(K) = 0$ ). Assume a catastrophe occurs at rate  $k(N)$  and with probability  $\hat{p}(i|N)$  between  $i$  and  $N - 1$  individuals die. Define

$$P_c(N) := \mathbb{P}(\text{population size is } N | \text{population not extinct}).$$

By considering the flow of individuals between populations of size  $N$  and  $N + 1$  at the

quasi-equilibrium, we obtain  $K - 1$  equations for the  $P_c(N)$ , namely

$$B(N)P_c(N) = D(N+1)P_c(N+1) + \sum_{i=N+1}^K k(i)\hat{p}(i-N|i)P_c(i). \quad (3.14)$$

We further demand the conditional probabilities sum to 1, i.e.

$$\sum_{N=1}^K P_c(N) = 1. \quad (3.15)$$

Thus (3.14) and (3.15) constitute a system of  $K$  equations in  $K$  unknowns and the conditional probability distribution is obtained by calculating the solution  $\mathbf{P}_c$  of the system

$$\begin{pmatrix} B(1) & -D(2)-k(2)p(1|2) & -k(3)p(2|3) & \dots & -k(K)p(K-1|K) \\ 0 & B(2) & -D(3)-k(3)p(1|3) & \dots & -k(K)p(K-2|K) \\ 0 & 0 & B(3) & \dots & -k(K)p(K-3|K) \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \dots & -D(K)-k(K)p(1|K) \\ 1 & 1 & 1 & \dots & 1 \end{pmatrix} \mathbf{P}_c = \begin{pmatrix} 0 \\ 0 \\ 0 \\ \vdots \\ 0 \\ 1 \end{pmatrix}$$

where  $p(i|N)$  denotes the probability that precisely  $i$  individuals die as a result of the disaster when the population has size  $N$ .

#### Example: *Eciton burchelli*

To illustrate the impact of catastrophes on population structure, we compare in figure 3-2 how the conditional population distribution for *Eciton burchelli* army ants depends on catastrophes. It is clear from this comparison that a frequently occurring catastrophe keeps the population well beneath the expected population level in the absence of such disasters. This suggests that disasters may dramatically shorten the expected time to extinction, so that their consideration in both field experiments and conservation

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programmes is crucial.

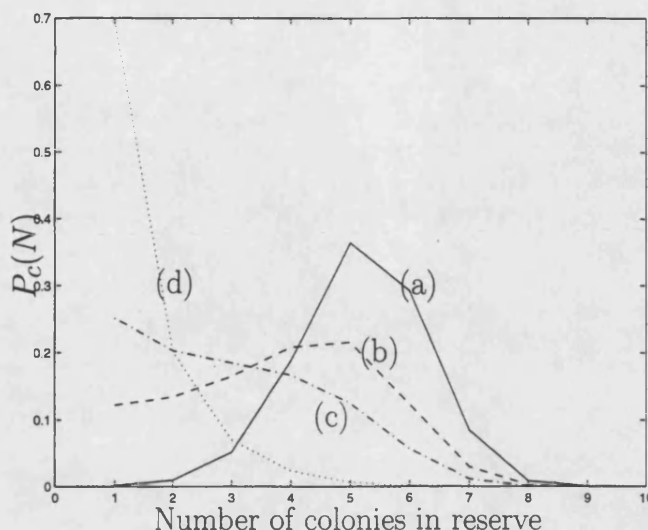


Figure 3-2: The conditional probability distribution as calculated by (3.14,3.15) for the number of *Eciton burchelli* colonies in a reserve of size  $K = 50$  depends strongly on catastrophes. The birth and death rates are those determined in section 3.2.1 with  $n = 6$ ,  $m = 5$  and  $\delta = 1/60$ , a reasonable figure (Partridge et al., 1996). (a) demonstrates the population distribution in the absence of catastrophes; the results of model (3.14,3.15) coincide with those of the algorithm of Nisbet and Gurney (1982). Catastrophes occur at rate  $k$  with (b)  $k = 0.05$ , (c)  $k = 0.1$  and (d)  $k = 0.5$ . During a catastrophe a colony dies with probability  $1/2$  so that deaths are binomially distributed. Catastrophes with  $k < 0.01$  have population distributions closely resembling populations subject to no catastrophes – there is sufficient time between catastrophes for the population to recover.

The predictions of this model are easily testable, simply by comparing temporal data on army ant abundance in various isolated reserves with equations (3.14) and (3.15).

### 3.2.3 Times to Extinction: A Markov Chain Model

Here we derive a simple model using general birth and death rates whose solution yields the expected time to extinction in the absence of catastrophes. Once this method is seen, the inclusion of catastrophes becomes straightforward. See Mangel and Tier (1993) (and also Mangel and Tier, 1994) for a similar model.

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## 3.2. BIRTH AND DEATH RATES, POPULATION DISTRIBUTIONS AND TIMES TO EXTINCTION

### A General Model

Consider a reserve currently occupied by  $n$  individuals. Denote the birth and death rates within the reserve as  $B(n)$  and  $D(n)$  respectively and let  $\tau(n)$  be a random variable denoting the extinction time. Write  $T(n) := \mathbb{E}[\tau(n)]$  as the expected time to reserve extinction.

Over a short interval of time  $\Delta t$ , there will either be a birth (with probability  $B(n)\Delta t$ ), a death (with probability  $D(n)\Delta t$ ) or else no change in population numbers. After this time has elapsed, we then expect to wait  $T(n+1)$ ,  $T(n-1)$  or  $T(n)$  until reserve extinction, depending on whether there was a birth, a death or neither event. The probability of, for example, two births during this time period is  $\mathcal{O}(\Delta t)$ . Hence the following equation is satisfied by all  $n > 0$ :

$$\begin{aligned} T(n) = & \Delta t + B(n)\Delta t T(n+1) + D(n)\Delta t T(n-1) \\ & + (1 - B(n)\Delta t - D(n)\Delta t)T(n) + \mathcal{O}(\Delta t), \end{aligned} \quad (3.16)$$

where the initial  $\Delta t$  arises since a small amount of time has elapsed before a possible birth or death. Rearranging (3.16), dividing by  $\Delta t$  and taking the limit as  $\Delta t \rightarrow 0$  yields the following system of linear equations for  $n > 0$ :

$$-1 = B(n)T(n+1) + D(n)T(n-1) - (B(n) + D(n))T(n). \quad (3.17)$$

When  $n = 0$  the population is extinct, hence the boundary condition  $T(0) = 0$ . If a population ceiling  $K$  is imposed in the reserve (so that  $B(K) = 0$ ), (3.17) reduces to a system of  $K$  linear equations in  $K$  unknowns and can be solved on a computer. This population ceiling need not be where density-dependent effects begin, nor is it the reserve's carrying capacity; it is simply some number which (greatly) exceeds the normal population size. In matrix notation, (3.17) takes the form

$$-1 = AT \quad (3.18)$$

where  $-1 \in \mathbb{R}^K$  denotes the vector with  $-1$  in each entry,  $T \in \mathbb{R}^K$  is the vector

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containing the expected extinction times and the matrix  $A$  is

$$\begin{pmatrix} -(B(1) + D(1)) & B(1) & 0 & \cdots & 0 \\ D(2) & -(B(2) + D(2)) & B(2) & \cdots & 0 \\ 0 & D(3) & -(B(3) + D(3)) & \ddots & \vdots \\ \vdots & \vdots & \ddots & \ddots & B(K-1) \\ 0 & 0 & \cdots & D(K) & -D(K) \end{pmatrix}.$$

The variance of the extinction times can also be found. The second moment of the extinction times  $S(n)$  is computed from  $S(n) = \mathbb{E}[\tau(n)^2]$ . Similar to the treatment for  $T(n)$  in (3.17),  $S(n)$  satisfies

$$-2T(n) = B(n)S(n+1) + D(n)S(n-1) - (B(n) + D(n))S(n) \quad (3.19)$$

so that in matrix form we have  $AS = -2T$ , which may be easily solved using computer packages such as MATLAB. The variance of the extinction time for a population with size  $n$ ,  $V(n)$ , can then be calculated component-wise from

$$V(n) = S(n) - T^2(n) \quad (3.20)$$

and the coefficient of variance is hence

$$CV(n) = \frac{\sqrt{V(n)}}{T(n)},$$

the latter providing a means of comparing the variability of extinction times for different populations (Mangel and Tier, 1993).

### Times to Extinction: Including Catastrophes

It is now very straightforward to include catastrophes in the model (3.17). As before, let  $B(n)$  and  $D(n)$  denote the birth and death rates respectively of a population. Suppose

that there exists a catastrophe which occurs at rate  $k(n)$  and with probability  $p(i|n)$ ,  $i$  individuals in a population currently numbering  $n$  will die as a result of the catastrophe. We demand, of course, that  $\sum_{i=0}^n p(i|n) = 1$  for all  $n \in \mathbb{N}$ .

In a similar fashion as before, let  $T(n)$  denote the expected time to extinction for a population currently supporting  $n$  individuals. Then for a small amount of time  $\Delta t$  we must have

$$\begin{aligned} T(n) = & \Delta t + B(n)\Delta t T(n+1) + D(n)\Delta t T(n-1) + k(n)\Delta t \sum_{i=0}^n p(i|n)T(n-i) \\ & + \{1 - B(n)\Delta t - D(n)\Delta t - k(n)\Delta t\} T(n) + \mathcal{O}(\Delta t). \end{aligned} \quad (3.21)$$

Rearranging, dividing by  $\Delta t$  and taking the limit as  $\Delta t \rightarrow 0$ , (3.21) reduces to the linear system of equations

$$\begin{aligned} -1 = & B(n)T(n+1) + D(n)T(n-1) + \sum_{i=0}^n k(n)p(i|n)T(n-i) \\ & - \{B(n) + D(n) + k(n)\} T(n) \end{aligned} \quad (3.22)$$

with the boundary condition  $T(0) = 0$ .

As before, by imposing a sufficiently high population ceiling,  $K$  say, (3.22) reduces to a system of  $K$  linear equations in  $K$  unknowns which can be written in the form

$$AT = -1 \quad (3.23)$$

where  $-1$  denotes the vector in  $\mathbb{R}^K$  with entries  $-1$  and  $A$  the matrix

$$\begin{pmatrix} -r(1) + k(1)p(0|1) & B(1) & 0 & \cdots \\ D(2) + k(2)p(1|2) & -r(2) + k(2)p(0|2) & B(2) & \cdots \\ k(3)p(2|3) & D(3) + k(3)p(1|3) & -r(3) + k(3)p(0|3) & \cdots \\ \vdots & \vdots & \vdots & \ddots \end{pmatrix} \quad (3.24)$$

where  $r(j) = B(j) + D(j) + k(j)$  denotes the event rate in the reserve when it supports  $j$  individuals. The variance of the extinction times can be easily shown to satisfy



equation (3.20) using the matrix  $A$  defined in (3.24).

### 3.2.4 Example: *Eciton burchelli*

As previously mentioned, sudden climatic changes, for example El Niño events, are the most common form of disasters affecting natural populations. Typically, the probability an individual survives a catastrophe is given by the outcome of a Bernoulli trial so that  $p(i|n)$ , the probability that  $i$  individuals die when the population is  $n$ , takes the form

$$p(i|n) = \binom{n}{i} \gamma^i (1 - \gamma)^{n-i}$$

where  $\gamma$  denotes the probability that a randomly selected individual will die under the catastrophe. Figures 3-3-3-5 show the expected extinction time from the quasi-equilibria for a variety of different binomial catastrophes on differing reserves sizes when the birth and death rates for *Eciton burchelli* army ants are applied to model (3.22). The equations are solved using the package MATLAB. The population ceiling  $K$  mentioned earlier has a natural interpretation here – it is simply the number of patches in a reserve since the number of army ant colonies can never exceed this value. In fact, see figure 3-1, the number of colonies will not in practice reach anywhere near this density.

### 3.2.5 Discussion of Markov Chain Model

The inclusion of catastrophes acting on a metapopulation can massively alter its expected time to extinction. This is best seen in figure 3-3 with catastrophe rate  $k = 10^{-1}$  where even disasters having low impact, i.e. small  $\gamma$ , can reduce expected persistence times by several orders of magnitude across all reserve sizes. As one would expect, the more frequent the disaster, the greater its reduction of persistence times. Clearly, since there is such a discrepancy between persistence times with and without catastrophes, their consideration in field studies and designing conservation programs cannot be stressed enough.

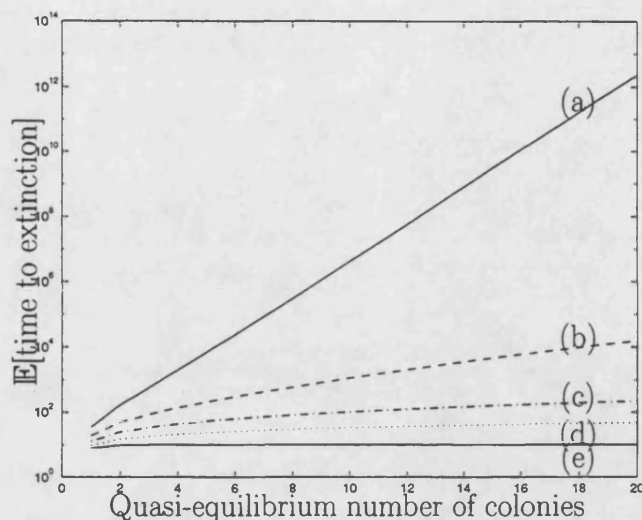


Figure 3-3: The expected time to reserve extinction in units of five week activity cycles is plotted as a function of the quasi-equilibrium number of colonies. Catastrophes occur at rate  $k = 0.1$ , i.e. on average every ten time units, and deaths are binomially distributed with mean  $\gamma$ . (a)  $\gamma = 0$  (no catastrophes), (b)  $\gamma = 0.25$ , (c)  $\gamma = 0.5$ , (d)  $\gamma = 0.75$  (e)  $\gamma = 1$ . In all instances the variance is also the expected time to extinction suggesting extinction times are exponentially distributed.

From a conservation viewpoint, these results make important suggestions in reducing extinctions. Should the disaster rate  $k$  lend itself to manipulation (e.g. if the disaster is a fire, one could reduce the risk of accidental fires), then even a small reduction of this parameter will greatly improve persistence times. Should  $k$  be beyond the reach of any conservation scheme (e.g. El-Niño or other climatic events), it is possible that the impact of the catastrophe,  $\gamma$ , may be altered. A reduction of this parameter can have significant effects, especially when the catastrophe rate is small (fig. 3-5). Mechanisms to reduce  $\gamma$  could range from capturing species prior to a disaster and releasing them afterwards to providing food or shelter in times of hardship (e.g. Lubow, 1996). Such schemes will be expensive, but in the expected time to extinction we have an index of the usefulness of a conservation method, which will both channel efforts into worthwhile programs and influence funding bodies.

Without exception, all the scenarios considered suggested extinction times were exponentially distributed, and in the words of Mangel and Tier (1994), this implies

### 3.2. BIRTH AND DEATH RATES, POPULATION DISTRIBUTIONS AND TIMES TO EXTINCTION

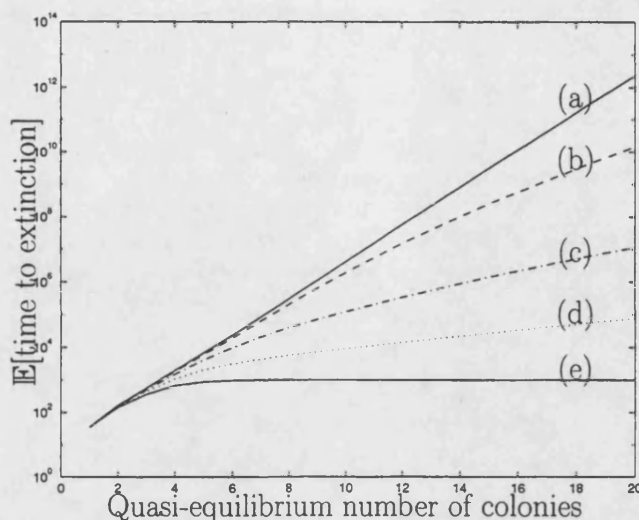


Figure 3-4: The expected time to reserve extinction in units of five week activity cycles is plotted as a function of the quasi-equilibrium number of colonies. Catastrophes occur at rate  $k = 10^{-3}$  and deaths are binomially distributed with mean  $\gamma$ . (a)  $\gamma = 0$  (no catastrophes), (b)  $\gamma = 0.25$ , (c)  $\gamma = 0.5$ , (d)  $\gamma = 0.75$  (e)  $\gamma = 1$ . In all instances the variance is also the expected time to extinction suggesting extinction times are exponentially distributed.

“extinctions are likely”. Given the model’s derivation, this is not a surprising result. It was assumed birth and death occurred via a Poisson process and so the expected times between events were exponentially distributed which, in turn, should imply extinction times are exponentially distributed. Whether extinction times have this distribution in general or is an artifact of the modelling assumptions is unknown.

This model may also be tested in the field. One requires a range of forest fragments which have been isolated from other remnants for a known time, and using the model one can calculate the probability each fragment currently supports a population of *Eciton burchelli*. In this fashion, the presence or absence of the army ants predicted by the model can be compared to field observations.

The model’s major disadvantage arises from the solution of the linear system of equations. For large carrying capacities, the system, even though it is relatively sparse, will be expensive to solve, requiring much time and computing power. A simple approximation may be desirable at times to avoid such monstrous calculations and two

### 3.2. BIRTH AND DEATH RATES, POPULATION DISTRIBUTIONS AND TIMES TO EXTINCTION

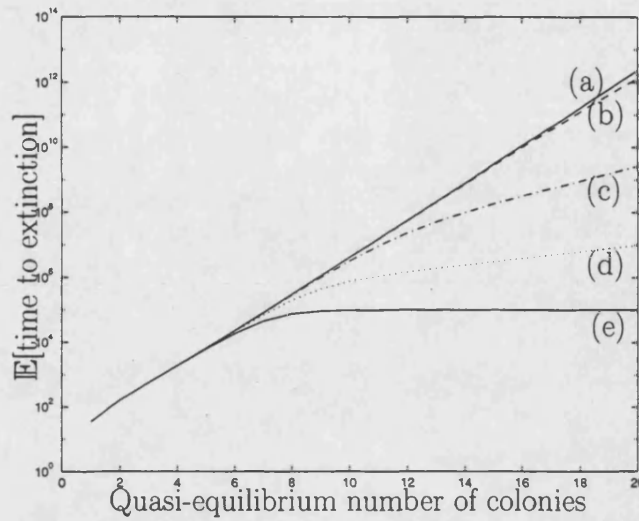


Figure 3-5: The expected time to reserve extinction in units of five week activity cycles is plotted as a function of the quasi-equilibrium number of colonies. Catastrophes occur at rate  $k = 10^{-5}$ , and deaths are binomially distributed with mean  $\gamma$ . (a)  $\gamma = 0$  (no catastrophes), (b)  $\gamma = 0.25$ , (c)  $\gamma = 0.5$ , (d)  $\gamma = 0.75$  (e)  $\gamma = 1$ . In all instances the variance is also the expected time to extinction suggesting extinction times are exponentially distributed.

such estimates are suggested in the following section.

### 3.3 Simple Analytical Approximations of Times to Extinction

For large reserves supporting many colonies, the calculation of the expected time to extinction using the Markov Chain model is expensive in terms of operations on the linear system (3.23). Thus a simple analytical approximation for this time is highly desirable.

#### 3.3.1 An Initial Analytical Approximation

Suppose, as in the previous model, a catastrophe occurs at rate  $k$  and kills each individual independently with probability  $\gamma$ . Assume for the moment  $k$  is sufficiently small compared to the expected time of recovery (i.e. the population can usually recover from

a catastrophe and return to the quasi-equilibrium state before another disaster). If  $n^*$  denotes the number of individuals at the quasi-steady state, the probability of a single catastrophe being responsible for extinction is  $\gamma^{n^*}$ . The rate this event occurs is simply  $k\gamma^{n^*}$ , making an approximation for the expected time to extinction

$$T = \frac{1}{k\gamma^{n^*}}. \quad (3.25)$$

### Comparison of the Initial Analytical Approximation with the Markov Chain Model

Using the results from figures 3-3-3-5 for reserves supporting 20 colonies at equilibrium, the expected time to extinction as calculated by the Markov Chain model is compared to that determined by the analytical approximation of (3.25). Table 3.1 illustrates these results and it is seen that the analytic approximation is good only for  $\gamma$  close to 1.

#### 3.3.2 An Improved Analytical Approximation

The initial approximation of section 3.3.1 can be greatly improved by noting the population with stochastic dynamics is not always at its quasi-equilibrium value; there is a probability distribution of population numbers. When the population is at a certain level, there is a probability a catastrophe could wipe out the entire population, e.g. when the population consists of  $N$  individuals, with probability  $p(N|N)$  the catastrophe forces the population extinct. By considering this distribution, the population death rate can be approximated from which an approximation of the expected time to extinction can be obtained.

With knowledge of the conditional population distribution  $P(i)$  (see e.g. §3.2.2), the population extinction rate can be approximated as

$$\psi = D(1)P(1) + k(1)p(1|1)P(1) + k(2)p(2|2)P(2) + k(3)p(3|3)P(3) + \dots \quad (3.26)$$

$k$	$\gamma$	MC (3.23,3.24)	Init. approx. (3.25)	Impr. approx. (3.27)
0	0	$3 \times 10^{12}$	— <sup>a</sup>	$3 \times 10^{12}$
$10^{-5}$	0.25	$1.3 \times 10^{12}$	$1 \times 10^{17}$	$2.3 \times 10^{12}$
	0.5	$2.6 \times 10^9$	$1 \times 10^{11}$	$3.1 \times 10^{10}$
	0.75	$9.7 \times 10^6$	$3 \times 10^7$	$2.6 \times 10^7$
	1	$1 \times 10^5$	$1 \times 10^5$	$1 \times 10^6$
$10^{-3}$	0.25	$1.4 \times 10^{10}$	$1 \times 10^{15}$	$1.6 \times 10^{12}$
	0.5	$1.1 \times 10^7$	$1 \times 10^9$	$3.2 \times 10^8$
	0.75	$7.7 \times 10^4$	$3 \times 10^5$	$2.6 \times 10^5$
	1	$1 \times 10^3$	$1 \times 10^3$	$1 \times 10^3$
$10^{-1}$	0.25	$1.5 \times 10^4$	$1 \times 10^{13}$	$5.8 \times 10^{10}$
	0.5	$2.2 \times 10^2$	$1 \times 10^7$	$3.2 \times 10^6$
	0.75	$4.8 \times 10^1$	$3 \times 10^3$	$2.6 \times 10^3$
	1	$1 \times 10^1$	$1 \times 10^1$	$1 \times 10^1$

Table 3.1: The expected time to extinction as calculated by the three different models for a reserve with parameters  $n = 6, m = 5, K = 200$  (i.e. the reserve supports 20 colonies at the quasi-equilibria) under a variety of catastrophes. Catastrophes occur at rate  $k$  and with probability  $\gamma$ , a colony dies as a result of the catastrophe. As before, time is measured in five week activity cycles, i.e. 10 cycles  $\approx$  1 year. Notice the initial approximation for the expected extinction time as calculated by (3.25) is good only when  $\gamma$  is close to 1. However, the improved analytical approximation, as calculated by equation (3.27) is in good agreement for most catastrophes. <sup>a</sup> the initial approximation is incapable of estimating this time.

and so the expected time to extinction is approximated by

$$T = \frac{1}{\psi}. \quad (3.27)$$

By using either of the methods outlined in section 3.2.2, the conditional distribution may be obtained. Notice, however, the algorithm of Nisbet and Gurney (1982) is an efficient and fast way of finding this distribution when disasters are rare. When disasters are common, their method fails and the only way of obtaining this distribution is by solving a large system of equations, just like the Markov Chain approach for expected extinction times, so that little is gained by an analytical approximation for the expected extinction time. We henceforth use the algorithm of Nisbet and Gurney (1982) to calculate the population distribution regardless of the catastrophe rate, knowing the algorithm gives good results for  $k < 0.01$  (see fig. 3-2).

### Results of Improved Approximation

In table 3.1 the improved analytical approximation (3.27) is compared to the Markov Chain model of section 3.2.3 and the previous initial approximation for binomially distributed catastrophes with the birth and death rates as calculated in section 3.2.1. It is clear that expression (3.27) gives a much better approximation of the expected extinction times than the initial model (3.25).

### 3.3.3 Discussion of Analytical Approximations

In the examples given above, the initial approximation which considered only the mean of the population numbers was seen to be in very good agreement with the MC model precisely when the catastrophe was very harsh – i.e. when it strikes, with a very high probability it forces the entire population extinct. This result is very much in line with intuition. However, under frequent catastrophes, the initial model gave significantly different results compared to the Markov Chain model; this relates to the model's neglect of population recovery.

The improved approximation, which considered the population distribution, could

account for disasters which removed only a few individuals and therefore increased the chance of population extinction. Thus expected extinction times calculated by this model closely resembled those predicted by the Markov Chain model unless the catastrophe was very frequent but having minimal impact.

Although not shown here, various sizes of reserves were examined and the expected time to extinction between the three models (MC, initial, improved) were compared. In all but the smallest of reserves, similar conclusions to the above were obtained; in such reserves, the MC model predicted faster extinctions than either of the approximations (3.25) or (3.27).

In the absence of catastrophes, the improved model (3.27) gave results in very good agreement with the MC model for all but the smallest of reserves. Using the iterative scheme of Nisbet and Gurney (1982) (see also section 3.2.2) this approximation for the expected extinction time is much cheaper to obtain than the estimate given by the Markov Chain model. However, under frequent catastrophes, using the method of section 3.2.2 to calculate conditional population distributions is rather pointless, since both the improved approximation for the expected extinction time (3.27) and the Markov Chain model (3.23) involve solving similar size systems whilst the former gives only an approximation of the later. Clearly, an efficient method of obtaining the conditional population distribution under disasters is required, although it is not the obvious extension of the algorithm presented in Nisbet and Gurney (1982), namely:

- (i) Choose population ceiling  $K \in \mathbb{N}$  where  $B(K)$  is sufficiently small
- (ii) Choose  $P(K)$  at random
- (iii) For  $i$  decreasing from  $K - 1$  to 1, set

$$P(i) = \frac{1}{B(i)} \left\{ D(i+1)P(i+1) + \sum_{j=i+1}^K k(j)\hat{p}(j-i+1|j)P(j) \right\} \quad (3.28)$$

- (iv) If  $P(K)$  is significantly different from  $\frac{P(K)}{\sum P}$ , set  $P(K) = \frac{P(K)}{\sum P}$  and repeat step (iii).

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### 3.3. SIMPLE ANALYTICAL APPROXIMATIONS OF TIMES TO EXTINCTION



The difficulty here arises in the calculation of  $P(K - 1)$  which, because of the small birth rates for populations near  $K$ , involves a division close to zero, and the algorithm fails. An efficient method of obtaining this distribution would be highly desirable.

### 3.4 Summary

In this chapter I initially gave examples of how catastrophes may greatly reduce persistence of species and how a measure of persistence which included disasters was required; the expected time to extinction was thus introduced. Various modelling techniques to calculate this important statistic were mentioned, and it was noted that only a few models were capable of estimating this value when the population underwent disasters.

In section 3.2.1 analytical expressions for the birth and death rates of *Eciton burchelli* colonies were developed and in the following subsection were used to examine the distribution of population numbers. With knowledge of the birth and death rates, using the Markov Chain model of Mangel and Tier (1993), the expected time to extinction for various reserves were calculated under a variety of catastrophes. It was seen that both the population distribution and the expected time to extinction were greatly altered by disasters.

A major difficulty of Mangel and Tier's model is that it often involves solving a massive system of linear equations which is expensive. To this end, in section 3.3 two analytical approximations were constructed for the expected time to extinction. The initial (and simplest) approximation was seen to be in good agreement with the MC model only when the catastrophe had a high probability of destroying all individuals at any one time. When the chance of this event is less, the initial model failed but the improved model made good predictions unless the disaster was frequent with low impact.

Overall it was seen that disasters have a massive impact on populations, and it is both surprising and worrying to note that so few models or conservation programmes account for them.

## Chapter 4

# Habitat corridors

Metapopulations, as created by habitat fragmentation, persist through a process of patch extinction followed by patch recolonisation (Hanski and Gilpin, 1991; Sabelis et al., 1991; Nee, 1994). Levins' classic metapopulation model (Levins, 1969, 1970) shows that persistence is prolonged either by reducing the patch extinction rate or by increasing the patch recolonisation rate. Habitat corridors, linear strips of vegetation connecting otherwise isolated patches, are designed to exploit the second of these. Such is their intuitive appeal, habitat corridors have been used around the world and form the basis of many conservation programs despite the dearth of supporting evidence. There have been recent suggestions in the literature (Soulé and Gilpin, 1991; Merriam, 1991; Hobbs, 1992; Bonner, 1994; Boswell et al., 1998, and see also chapter 2) that corridors could reduce metapopulation persistence times by allowing the transmission of disasters (for example, diseases or forest fires) or by the corridor acting as a demographic sink. These important suggestions remain untested in any form; they are addressed through mathematical modelling in this chapter.

In section 4.1 the definition of a habitat corridor is given for the purpose of this investigation. From this, it is shown how island biogeographic, and Levin's metapopulation model in particular, advocate the use of habitat corridors. Reference is then made to other studies, both theoretical and empirical, concerned with habitat corridors. It is noted that empirical studies are typically flawed; usually by demonstrating

that a corridor is used by a species, not how it affects species persistence. An argument is then constructed, based on the results of chapter 2, which claims habitat corridors are not always beneficial, they can worsen metapopulation persistence. The computer simulation of section 2.3 for *Eciton burchelli* army ants is extended in section 4.2 for simple habitat corridor arrangements. It is seen the aforesaid argument holds. A general model using Markov Chains is then developed in section 4.3 to predict the expected time to metapopulation extinction and parameter values similar to *Eciton burchelli* army ants are applied. The conclusions of this model agree with those of the simulation model. The practical uses of the Markov Chain model are shown to be limited, and in section 4.4 a stochastic differential equation model is derived. Properties of this SDE model, including an approximation for the expected extinction time, are obtained. The behaviour of this model is compared with the previous two, and is seen to have numerous similarities, and in particular, it is noted certain corridors reduce metapopulation persistence.

## 4.1 History of Corridors

For the purpose of this chapter a *habitat corridor* (or *conservation corridor* or *wildlife corridor*) is defined to be a linear two-dimensional landscape element joining two patches of (animal) habitat which have been historically connected; it is meant to function as a conduit for animal dispersal. It can either be a natural feature, such as a river bank, or an artificial element, for example a hedgerow or a road verge.

Whilst certain wildlife corridors can act as habitat in its own right, we shall here be primarily concerned with the dispersal corridor principle, i.e. a corridor simply providing a means of travelling from *A* to *B* across an otherwise hostile landscape. Thus the corridor acts to increase dispersal between any two habitat patches.

The theoretical arguments advocating the use of wildlife corridors are simple, being based around island biogeographic models (MacArthur and Wilson, 1967; Wilson and Willis, 1975), or equivalently, as we shall present here, metapopulation models.

### 4.1.1 Habitat Corridors: The Theory

Recall Levins' metapopulation model (2.1) of chapter 2. It says if there exists an infinite number of identical habitat patches, a proportion  $p$  of which are occupied, then if  $e$  denotes the patch extinction rate and  $c$  the rate a patch emits colonisers, the rate of change of occupied patches is given by

$$\frac{dp}{dt} = cp(1 - p) - ep$$

and the non-trivial steady state, should it exist, is given by

$$p^* = 1 - \frac{e}{c}. \quad (4.1)$$

When the number of patches is finite, stochastic effects alone mean the metapopulation will eventually go extinct (Karlin and Taylor, 1981; Nisbet and Gurney, 1982), the only issue being how long extinction takes. By increasing the quasi-equilibria  $p^*$  described by (4.1), the expected time to extinction is prolonged (Nisbet and Gurney, 1982, see also chapter 3). This can be achieved either by (i) decreasing the patch extinction rate  $e$ , or by (ii) increasing the patch recolonisation rate  $c$ . Conservation corridors are designed to exploit the second of these. Indeed, this approach leads to such conclusions as Edward Wilson's and Edwin Willis's in 1975:

“Extinctions will be lower when fragments can be connected by corridors of natural habitat, no matter how thin the corridors.”

Whilst the theoretical arguments supporting corridors are clear, there are numerous possible disadvantages:

**Spreading disasters** The existence of a corridor connecting two subpopulations could allow a disaster in one habitat patch to occur in another. For example, a diseased disperser might induce an epidemic to another patch; a woodland corridor may encourage a forest fire to spread (Hobbs, 1992; Hess, 1996a).

**Expensive conservation tools** Given the typical geography of corridors – long narrow linear strips – they are usually very expensive to establish and maintain. It is therefore necessary to demonstrate to funding bodies that a corridor can significantly reduce extinctions (Simberloff and Cox, 1987).

**Connecting to sinks** If a corridor connects a viable habitat patch to an unviable patch, overall persistence, it is argued, could be reduced by the second patch acting as a demographic sink (Merriam, 1991).

**Corridors as sinks** As an extension of the above point, it has been suggested that a corridor itself could act as a demographic sink. A higher death rate within the corridor may be caused, for example, by poorer quality habitat or increased predation. Indeed, by referring to the fractal dimension work of chapter 2, one can observe that a corridor, having a low fractal dimension, acts as a very poor reserve and, further, could act as a demographic sink (Soulé and Gilpin, 1991; Boswell et al., 1998).

Thus in Levins' metapopulation model, not only is the patch recolonisation rate  $c$  a function of the corridor, but the patch extinction rate  $e$  may also depend somehow on the corridor.

#### 4.1.2 Habitat Corridors: Empirical Studies

Nature corridors have been widely used around the world and form an integral part of many conservation schemes (Brooker et al., 1999). Yet, despite their widespread use, there is little empirical evidence supporting corridors (but see Ims and Stenseth, 1989; Gilbert et al., 1998). Upon examining the literature, one discovers that practically all studies on corridor assessment simply examine whether or not the corridor increases inter-patch dispersal (e.g. Hussey, 1991; Nicholls and Margules, 1991; Bennett, 1991; Lynch and Saunders, 1991; Wardell-Johnson and Roberts, 1991; Catterall et al., 1991; Preveit, 1991; Arnold et al., 1991; Brooker et al., 1999). This is not sufficient to show corridors reduce extinction; it may be that a corridor, as well as increasing dispersal

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### 4.1. HISTORY OF CORRIDORS

rates, could also increase patch extinction rates. So by simply showing that animals prefer to use a corridor rather than the surrounding habitat matrix, one does not show how this relates to metapopulation, or even patch, extinction rates. A broader study is clearly necessary, one considering the entire metapopulation rather than just a few individuals in a corridor.

A few empirical studies do answer the corridor question, for example, Ims and Stenseth (1989) and Gilbert et al. (1998), but there are no studies for those species which specifically require conservation. It has been shown that microecosystems (i.e. bacterial communities) benefit from corridor connections (Kruess and Tsharntke, 1994), but the differences between bacteria and, for example, chimpanzees are immense.

It has been shown, however, that corridors can suffer higher predation rates than continuous habitat – suggesting the demographic sink case above – simply because the predator is an edge specialist. For example, in Florida, it has been found that Diamond-back snakes have higher densities in corridors than in more continuous habitats since many of their prey items (rodents) choose to use corridors as a means of dispersal (Mann, 1995).

#### 4.1.3 Modelling the Simplest Corridor

Clearly, empirical studies are necessary to determine whether corridors can reduce extinctions, but the numerous problems (especially with experimental design) make such studies difficult. To this end, mathematical models focus attention on a few parameters which should be easier to obtain in the field, and from these models, experiments will hopefully be suggested.

In order to obtain general and useful results, the models shall focus on the simplest metapopulation/habitat corridor scenario; a two-patch metapopulation or a dumbbell reserve. The models, where appropriate, shall be initially derived for general  $K$ -patch reserves but, for simplicity, the analysis shall deal specifically with the 2-patch case (see also Nisbet et al., 1993; Hastings, 1993; Tishendorf and Wissel, 1997).

## 4.2 A Computer Simulation of a Dumbbell Reserve

The first model is a spatially realistic computer simulation of the army ant *Eciton burchelli*. In fact, it is precisely the same computer program as in chapter 2, only with a different arena.

### 4.2.1 Simulation Description

The simulation arena is chosen to be a dumbbell as shown in figure 4-1, each patch having an area of roughly  $1\text{km}^2$ . The patches are positioned at varying distance apart, ranging from 360 metres up to about 7 km; the patches then being connected by corridors of varying widths (180m, 360m, 540m). Four colonies, approximately the quasi-equilibrium number according to chapter 2, are then randomly distributed in each pocket and the system is allowed to evolve according to the usual rules as specified in section 2.3.1 until extinction. For each corridor design, 1000 runs to extinction are undertaken and the time to extinction recorded. As a comparison, the mean time to extinction for two unconnected patches is also obtained – the distance between such patches being irrelevant.

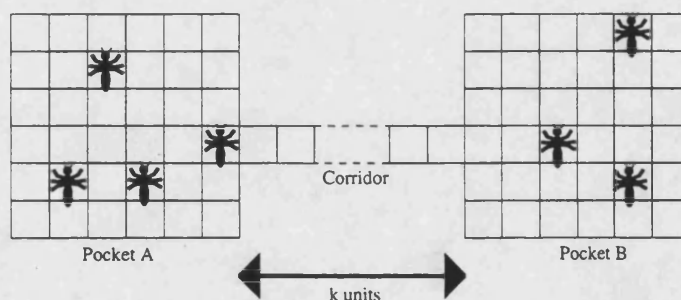


Figure 4-1: The simulation arena is a two-patch reserve, or dumbbell, and the simulation is a variant of that of section 2.3.1. Each small square denotes an area of rain forest 180m by 180m, so that the two habitat patches are each roughly  $1\text{km}^2$  in area. The distances between the pockets is varied between 360 metres and about 7km. The patches are then joined at the middle of one side by a corridor of varying widths, in this instance 180 metres.

### 4.2.2 Results of Simulation

#### Corridors of Width 180m

When the two pockets are connected by a 180m-wide corridor, the expected times to extinction are those seen in figure 4-2. Notice that if the pockets are reasonably close together, less than 1 km, the construction of a narrow corridor will improve persistence times considerably. Should the pockets be approximately 1km apart, the establishment of a narrow corridor will make little difference to the expected time to extinction. However, if the corridors are a considerable distance apart, a narrow corridor will significantly reduce metapopulation persistence. The long narrow corridor is acting as a population sink; once a colony enters the corridor it undergoes a random walk continually visiting recently raided areas (c.f. chapter 2), thus increasing its chances of starvation. We thus have a contradiction to the statement of Wilson and Willis of section 4.1.

#### Corridors of Width 360m

If the corridor is widened, any colony within the corridor should have access to more unraided areas and so should fair better than compared to a narrower passage. This is confirmed by the results of figure 4-3. Notice persistence is greatly improved by this wider corridor compared to the narrower corridor of fig 4-2.

#### Corridors of Width 540m

If the corridor is widened still further, as one would expect, the mean time to metapopulation extinction is also increased (Fig 4-4).

### 4.2.3 Discussion of Simulation Model

The simulation model has shown that habitat corridors can either promote or prevent extinctions; the design of the corridor influencing which of these events occurs. For *Eciton burchelli* army ants, a internal-forest specialist, we have seen that the corridor



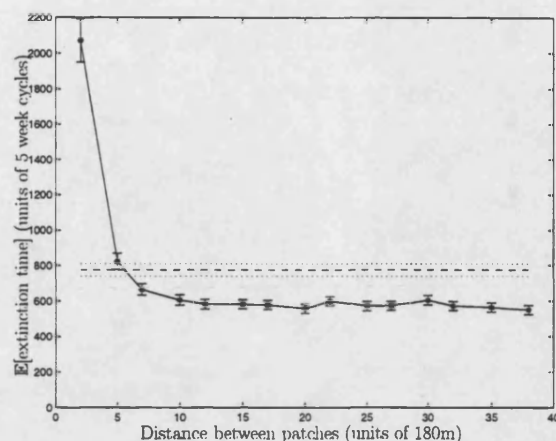


Figure 4-2: The time to dumbbell extinction using a corridor 180 metres wide is plotted as a function of the distance between the two patches. The mean time of 1000 runs is shown for each corridor length (solid line) along with 95% confidence intervals. As a comparison, the mean time of 1000 runs in the absence of a corridor is also shown (dashed line) with 95% confidence intervals (dotted lines). Notice that it is better for nearby patches to be connected than remain isolated (e.g. for patches 360 metres apart it is significantly better to be connected than separate, one-way ANOVA tests  $p < 0.0001$ ); but for distant patches, i.e. those further than 2km apart, the inclusion of a corridor of width 180m significantly worsens the persistence time (e.g. for patches 4km apart again the difference is significant, one-way ANOVA tests  $p < 0.0001$ .)

ought to be as wide as possible. Referring back to the fractal dimension work of chapter 2, it was seen the optimal reserves were those of largest area and largest fractal dimension. In this setting, the best corridors will thus be those of largest fractal dimension, i.e. those having greatest width.

Another point worth noting is that dumbbell extinction times are asymptotic with regards to corridor length (see, e.g. fig. 4-2). For a given corridor width, as the distance between the patches is increased, the expected extinction time tends towards a limit (which is that associated with a corridor in which no colonies successfully travel through it, some die whilst the remaining colonies return to the initial patch).

These fundamental characteristics ought to be reflected in both field data (which would certainly be hard to test) and, especially, other mathematical models (which should be much more accessible).

#### 4.2. A COMPUTER SIMULATION OF A DUMBBELL RESERVE

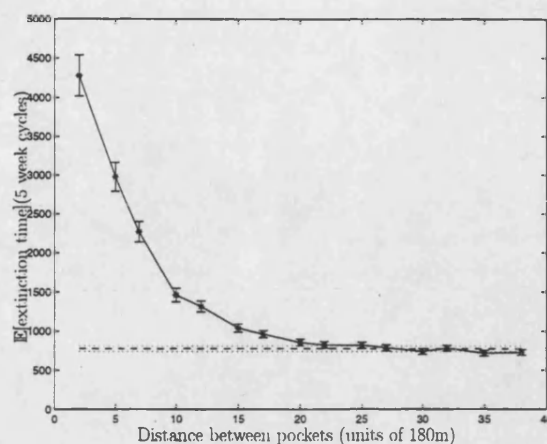


Figure 4-3: The time to extinction using a corridor 360m wide is plotted as a function of the distance between the two patches. The mean of 1000 runs is shown for each patch distance (solid line), along with 95% confidence intervals. As a comparison, the expected extinction time in the absence of a corridor (dashed line) is also shown again with 95% confidence intervals (dotted lines). Notice that persistence is prolonged by this wider corridor compared to the narrower corridor of fig 4-2.

### 4.3 A Markov Chain Model

In the above section, we saw that a spatially realistic computer simulation gave rise to some extremely interesting and potentially very important results concerning habitat corridors for *Eciton burchelli*. Should similar conclusions be reached about corridors with other species, many conservation programmes around the world ought to be heavily revised. The difficulty with the previous approach is that a computer simulation would have to be written and performed for a large number of species – an enormous task for those concerned. Thus a general mathematical model is desirable; one whose parameters are relatively straightforward to obtain in the field. We shall develop such a model here. The model is very simple, requiring only the birth and death rates within the habitat patches and knowledge of the species' behaviour in and around the corridor. The model is in essence an extension to multi-patch reserves of the single patch model of Mangel and Tier (1993) (see also Mangel and Tier, 1994) and that of chapter 3.

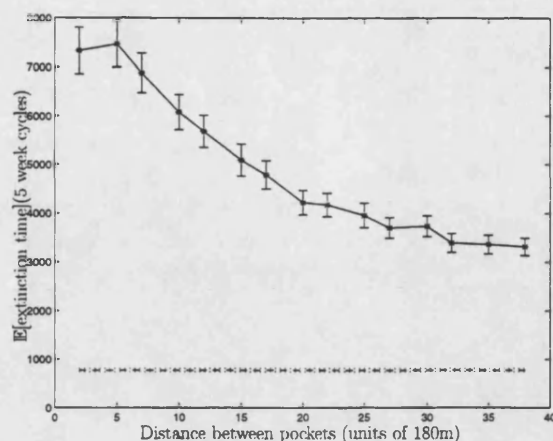


Figure 4-4: The time to extinction using a corridor 540m wide is plotted as a function of the distance between the two patches. The mean of 1000 runs is shown for each patch distance (solid line), along with 95% confidence intervals. As a comparison, the expected extinction time in the absence of a corridor (dashed line) is also shown, again with 95% confidence intervals (dotted lines). Notice that persistence is prolonged by this wider corridor compared to the narrower corridors of figs 4-2 & 4-3. Corridors of this width begin to be habitat in their own right (i.e. capable of supporting an *Eciton burchelli* population).

#### 4.3.1 Derivation of Model

Consider a  $K$ -patch metapopulation which is connected by corridors, such as that in figure 4-5.

Let the vector  $\mathbf{n}(t)$  describe the state of the metapopulation at time  $t$  where  $n_i \in \mathbb{N}$  denotes the number of individuals in patch  $i$ . Suppose the birth and death rates in patch  $i$  are described by  $b_i(\mathbf{n})$  and  $d_i(\mathbf{n})$  respectively. Let  $c_{ij}(\mathbf{n})$  denote the rate at which individuals enter a corridor connecting patch  $j$  to patch  $i$  (that is the rate at which individuals leave patch  $i$  initially bound for patch  $j$ ). In the case of no connecting corridor between patches  $i$  and  $j$ ,  $c_{ij}$  is simply zero (fig 4-5). Let  $p_{ij}(\mathbf{n})$  denote the probability an individual passes through the corridor from patch  $i$  to patch  $j$  and  $r_{ij}(\mathbf{n})$  is the probability it dies. Thus with probability  $1 - (p_{ij} + r_{ij})$  the individual returns to the patch of dispersal. Now let  $T(\mathbf{n})$  denote the expected time to metapopulation extinction when the metapopulation is in state  $\mathbf{n}$ . Using a random walk argument

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#### 4.3. A MARKOV CHAIN MODEL

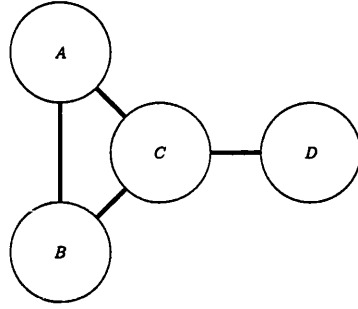


Figure 4-5: A metapopulation is spread over  $K = 4$  patches. Each patch can support a population, but the birth and death rates in each patch may be different. Corridors exist connecting certain patches, thus allowing the movement of individuals from one patch to another. In this fashion, a population going extinct in patch  $A$ , say, can be restarted by the arrival of a disperser from either patch  $B$  or patch  $C$ . Since there is no corridor connecting  $A$  to  $D$ , the colonisation rate from  $A$  to  $D$ ,  $c_{AD}$ , is zero.

similar to that seen in section 3.2.3, it is easily seen that

$$\begin{aligned}
 T(\mathbf{n}) = & \Delta t + \sum_{i=1}^K b_i(\mathbf{n}) \Delta t T(\mathbf{n} + \mathbf{e}_i) + \sum_{i=1}^K d_i(\mathbf{n}) \Delta t T(\mathbf{n} - \mathbf{e}_i) \\
 & + \sum_{i,j=1, i \neq j}^K c_{ij}(\mathbf{n}) p_{ij}(\mathbf{n}) \Delta t T(\mathbf{n} - \mathbf{e}_i + \mathbf{e}_j) + \sum_{i,j=1, i \neq j}^K c_{ij}(\mathbf{n}) r_{ij}(\mathbf{n}) \Delta t T(\mathbf{n} - \mathbf{e}_i) \\
 & + \left\{ 1 - \sum_{i=1}^K (b_i(\mathbf{n}) + d_i(\mathbf{n})) \Delta t - \sum_{i,j=1, i \neq j}^K c_{ij}(\mathbf{n}) [p_{ij}(\mathbf{n}) + r_{ij}(\mathbf{n})] \Delta t \right\} T(\mathbf{n}) \\
 & + o(\Delta t)
 \end{aligned} \tag{4.2}$$

where  $\mathbf{e}_i$  denotes the vector in  $\mathbb{R}^K$  with a '1' in the  $i^{\text{th}}$  entry and '0' elsewhere. Rearranging the above formula, dividing by  $\Delta t$  and taking limits as  $\Delta t \rightarrow 0$ , we arrive at the following system of linear equations

$$\begin{aligned}
 -1 = & \sum b_i(\mathbf{n}) T(\mathbf{n} + \mathbf{e}_i) + \sum d_i(\mathbf{n}) T(\mathbf{n} - \mathbf{e}_i) \\
 & + \sum c_{ij}(\mathbf{n}) p_{ij}(\mathbf{n}) T(\mathbf{n} - \mathbf{e}_i + \mathbf{e}_j) + \sum c_{ij}(\mathbf{n}) r_{ij}(\mathbf{n}) T(\mathbf{n} - \mathbf{e}_i) \\
 & - \left\{ \sum [b_i(\mathbf{n}) + d_i(\mathbf{n})] + \sum c_{ij}(\mathbf{n}) [p_{ij}(\mathbf{n}) + r_{ij}(\mathbf{n})] \right\} T(\mathbf{n})
 \end{aligned} \tag{4.3}$$

where the limits of summation are those in equation (4.2).

### 4.3. A MARKOV CHAIN MODEL

If we now suppose that patch  $i$  has a population ceiling of  $N_i$  individuals, then (4.2) is simply a system of  $\prod_{i=1}^K (N_i + 1)$  linear equations which can be solved on a computer using the obvious boundary condition  $T(\mathbf{0}) = 0$ .

An important point to note is that the  $N_i$  must be significantly larger than the usual population size of patch  $i$  (i.e.  $N_i > \widetilde{N}_i$  where  $b_i(\widetilde{N}_i) = d_i(\widetilde{N}_i)$ ). This is crucial since immigration to patch  $i$  could temporarily force the population to higher than normal levels.

We can write (4.3) as the matrix equation  $-1 = AT$ . Second order moments,  $S$ , are derived similar to the first moments considered in (4.2) and as in section 3.2.3 are seen to be the solution of the linear system  $AS = -2T$  so that the variance  $V(\mathbf{n})$  of extinction times for metapopulations initially of size  $\mathbf{n}$  can be computed component-wise using

$$V(\mathbf{n}) = S(\mathbf{n}) - T^2(\mathbf{n}), \quad (4.4)$$

and the coefficient of variation is hence given by

$$CV(\mathbf{n}) = \frac{\sqrt{V(\mathbf{n})}}{T(\mathbf{n})}.$$

### Catastrophes are Important

In Chapter 3 it was shown that catastrophes, events of mass population decline, can have a significant effect on population persistence. Simberloff (1988), Mangel and Tier (1994) and Ludwig (1999), for example, all state that models of extinctions must consider such population disasters. In the Markov Chain model their inclusion is straightforward, much like it was in chapter 3. For simplicity, in the remainder of this section we shall consider  $K = 2$ , the simplest metapopulation/habitat corridor scenario.

There are, in essence, two types of catastrophes which can affect a 2-patch reserve. The first is one which affects both patches simultaneously, regardless of them being connected by a corridor; we shall call these Type I catastrophes. Type II catastrophes will hit each patch independently of the other, again regardless of the existence of a

connecting corridor. Thus, and as an aid to memory, *one* type I catastrophe will affect the whole metapopulation, while at least *two* type II catastrophes are required to do likewise.

### Type I Catastrophes : $K = 2$

Suppose a type I catastrophe occurs at rate  $k(n_1, n_2)$  where  $n_1$  and  $n_2$  are the number of individuals in patches 1 and 2 respectively, and with probability  $p(i, j|n_1, n_2)$ ,  $i$  and  $j$  individuals in patches 1 and 2 die respectively. (Of course, we demand  $\sum_{i=0}^{n_1} \sum_{j=0}^{n_2} p(i, j|n_1, n_2) = 1$ .) Then by including the additional term

$$k(n_1, n_2) \sum_{i=0}^{n_1} \sum_{j=0}^{n_2} p(i, j|n_1, n_2) T(n_1 - i, n_2 - j) \quad (4.5)$$

in (4.2) – the derivation of the model – one arrives at the system

$$\begin{aligned} -1 = & b_1(\mathbf{n})T(n_1 + 1, n_2) + b_2(\mathbf{n})T(n_1, n_2 + 1) + d_1(\mathbf{n})T(n_1 - 1, n_2) \\ & + d_2(\mathbf{n})T(n_1, n_2 - 1) + c_{12}(\mathbf{n})p_{12}(\mathbf{n})T(n_1 - 1, n_2 + 1) \\ & + c_{12}(\mathbf{n})r_{12}(\mathbf{n})T(n_1 - 1, n_2) + c_{21}(\mathbf{n})p_{21}(\mathbf{n})T(n_1 + 1, n_2 - 1) \\ & + c_{21}(\mathbf{n})r_{21}(\mathbf{n})T(n_1, n_2 - 1) \\ & + k(\mathbf{n}) \sum_{i=0}^{n_1} \sum_{j=0}^{n_2} p(i, j|n_1, n_2) T(n_1 - i, n_2 - j) \\ & - \{b_1(\mathbf{n}) + b_2(\mathbf{n}) + d_1(\mathbf{n}) + d_2(\mathbf{n}) + c_{12}(\mathbf{n})[p_{12}(\mathbf{n}) + r_{12}(\mathbf{n})] \\ & + c_{21}(\mathbf{n})[p_{21}(\mathbf{n}) + r_{21}(\mathbf{n})] + k(\mathbf{n})\} T(n_1, n_2). \end{aligned} \quad (4.6)$$

Notice the catastrophe does not alter the number of equations in the system, so its inclusion does not lead to a significantly harder or more expensive system to be solved, although of course, the system will be less sparse as there are clearly more non-zero entries in the matrix.

**Type II Catastrophes :  $K = 2$** 

Recall a type II catastrophe occurs in patches 1 and 2 independently. Suppose a type II catastrophe occurs in patch  $i$  at rate  $k_i(n_i)$ , and when it does, with probability  $p_i(j|n_i)$ ,  $j$  individuals die in that patch. Then by including the additional terms

$$k_1(n_1) \sum_{i=0}^{n_1} p_1(i|n_1) T(n_1 - i, n_2) + k_2(n_2) \sum_{i=0}^{n_2} p_2(i|n_2) T(n_1, n_2 - i) \quad (4.7)$$

in (4.2) – the derivation of the model – the following system is obtained

$$\begin{aligned} -1 = & b_1(\mathbf{n})T(n_1 + 1, n_2) + b_2(\mathbf{n})T(n_1, n_2 + 1) \\ & + d_1(\mathbf{n})T(n_1 - 1, n_2) + d_2(\mathbf{n})T(n_1, n_2 - 1) \\ & + c_{12}(\mathbf{n})p_{12}(\mathbf{n})T(n_1 - 1, n_2 + 1) \\ & + c_{12}(\mathbf{n})r_{12}(\mathbf{n})T(n_1 - 1, n_2) + c_{21}(\mathbf{n})p_{21}(\mathbf{n})T(n_1 + 1, n_2 - 1) \\ & + c_{21}(\mathbf{n})r_{21}(\mathbf{n})T(n_1, n_2 - 1) + k_1(n_1) \sum_{i=0}^{n_1} p_1(i|n_1)T(n_1 - i, n_2) \\ & + k_2(n_2) \sum_{i=0}^{n_2} p_2(i|n_2)T(n_1, n_2 - i) - \{b_1(\mathbf{n}) + b_2(\mathbf{n}) + d_1(\mathbf{n}) + d_2(\mathbf{n}) \\ & + c_{12}(\mathbf{n})[p_{12}(\mathbf{n}) + r_{12}(\mathbf{n})] + c_{21}(\mathbf{n})[p_{21}(\mathbf{n}) + r_{21}(\mathbf{n})] \\ & + k_1(n_1) + k_2(n_2)\} T(n_1, n_2). \end{aligned} \quad (4.8)$$

Again notice the inclusion of this catastrophe does not increase the size of the system and so is not significantly more expensive to solve than the model without catastrophes, although, again, the system will be less sparse.

**4.3.2 Parameter Estimation**

As in section 4.2, we consider *Eciton burchelli* army ants in a dumbbell reserve. However, for analytical reasons yet to be seen, we shall focus attention on the “stepping” army ant colonies as discussed in Britton et al. (1996). These are identical in every respect to the army ants discussed previously, only their powers of dispersal are less. Indeed, rather than move to any of the 24 squares at the edge of a  $7 \times 7$  square whose

centre is the current position, the stepping army ants can only move to the eight squares on the edge of a  $3 \times 3$  square whose centre is the current position (see fig. 2-2). The differences between these dynamics and mean field dynamics are small (fig. 2-3(c)), hence within the habitat pockets we assume the birth and death rates are those associated with mean field dynamics. Also, for simplicity, we shall ignore queen death.

### Birth and Death Rates

The birth and death rates are simply those derived in chapter 3 for mean field dynamics with  $\delta = 0$  (i.e. no queen death). This is a good approximation for the stepping army ant colonies as seen in fig. 2-3(c).

### Population Ceilings

Due to the nature of the model, there cannot be more colonies in a habitat pocket than there are square patches. To be consistent with section 4.2 we choose  $N_1 = N_2 = 36$  as in figure 4-1. Notice this population ceiling is significantly higher than the quasi-equilibrium number of colonies (about 4), as was earlier demanded (see page 85).

### Corridor Entrance Rate

Given the assumption of stepping dynamics, the only way for a colony to enter the corridor is from any one of the three patches around its entrance (fig 4-6). From the assumption of mean field dynamics within habitat pockets, if there are  $n$  colonies in the pocket then the probability that a given patch is occupied is simply  $n/36$ . Thus a first order approximation is reasonable (since  $n/36$  is most likely small from chapter 2), and the corridor entrance rate is thus  $3 \times n/36 \times 1/8$  since the corridor can be entered from three squares each with probability  $1/8$ . In this sense, the corridor entrance rate is density-independent – a reasonable assumption given the spatial dynamics of army ants.



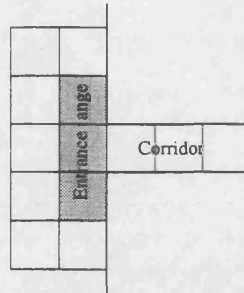


Figure 4-6: We assume a colony in one cell can move only to its eight adjacent neighbouring cells. Thus to first order, the probability the corridor is entered is simply the probability any of the corridor entrance range squares is occupied multiplied by the probability that the move takes it into the corridor.

### Corridor Outcome Probabilities – Corridors 180 Metres Wide

For corridors of 180 metres in width, we can construct an analytical approximation for the corridor outcome probabilities using the analytical model of chapter 2 and Britton et al. (1996) for the “stepping” ant colonies. For wider corridors, this analysis cannot work – the system becomes non-Markov which complicates the necessary mathematics considerably.

Suppose the corridor is  $k$  patches long (i.e.  $180 \times k$  metres). As in the model of chapters 2 & 3, patches exist in two states – either plentiful or exhausted of their resources. A colony encountering a plentiful patch grows one unit in size (about 60 000 worker ants) whereas a colony landing on an exhausted patch decreases one unit in size. A colony of size 0 is assumed dead and, since we are only considering dispersal corridors in this chapter, we shall neglect the possibility of colony birth in the corridor, an assumption we shall later justify. A colony in the corridor undertakes a random walk, moving forwards and backwards with probabilities  $\lambda$  and  $\nu$  respectively ( $\lambda + \nu = 1$ ). We shall assume that upon entering the corridor, all patches are plentiful in resource; once a patch has been visited, it remains depleted for the duration the colony is in the corridor. Since in a random walk, the colony will spend much time wandering back and forth over a small region (Feller, 1967) (especially if  $\lambda = \nu = 1/2$ , the case we will be interested in) the disregard of patch recovery is reasonable (see also table 4.1). The

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### 4.3. A MARKOV CHAIN MODEL

assumption that all patches are initially plentiful of prey is valid as long as the corridor entrance rate is sufficiently small. The colony size will hence be bounded above by  $\tilde{m} + k$ , its initial size,  $\tilde{m}$ , plus the number of patches. A colony will be very unlikely to reach this size due to the nature of a random walk and so the disregard of corridor birth is justifiable.

Let  $p_k(\gamma, x, y)$  denote the probability a colony of size  $\gamma$  will successfully reach the end of the corridor of length  $k$  given that it is  $x$  patches away from its goal,  $y$  of which are depleted patches. In fact, the  $y$  patches immediately in front of the colony will be depleted as well as the  $k - x - 1$  patches behind and the patch currently occupied. Hence  $p_k(\gamma, x, y)$  will satisfy

$$p_k(\gamma, x, y) = \nu p_k(\gamma - 1, x + 1, y + 1) + \begin{cases} \lambda p_k(\gamma + 1, x - 1, 0) & \text{if } y = 0 \\ \lambda p_k(\gamma - 1, x - 1, y - 1) & \text{otherwise} \end{cases} \quad (4.9)$$

with boundary conditions

$$\begin{aligned} p_k(0, \cdot, \cdot) &= 0 & (\text{colony starves}) \\ p_k(\cdot, 0, \cdot) &= 1 & (\text{colony successful}) \\ p_k(\cdot, k + 1, \cdot) &= 0 & (\text{colony returns to start}). \end{aligned} \quad (4.10)$$

Let  $q_k(\gamma, x, y)$  denote the probability the colony will return to the start. Then  $q_k$  will also satisfy (4.9) but with boundary conditions

$$\begin{aligned} q_k(0, \cdot, \cdot) &= 0 \\ q_k(\cdot, 0, \cdot) &= 0 \\ q_k(\cdot, k + 1, \cdot) &= 1. \end{aligned} \quad (4.11)$$

Similarly, if  $r_k(\gamma, x, y)$  denotes the probability of death in the corridor,  $r_k$  satisfies

Corridor length	$p$	$q$	$r$	$p_{sim}$	$q_{sim}$	$r_{sim}$
5	0.1215	0.7682	0.1169	0.1390	0.7640	0.1290
10	0.0295	0.7728	0.2065	0.0430	0.7840	0.2010
15	0.0069	0.7729	0.2230	0.0180	0.7760	0.2170
20	0.0019	0.7729	0.2262	0.0060	0.7800	0.2180

Table 4.1: The probabilities  $p$  (successful passage),  $q$  (return to start), and  $r$  (corridor death) are functions of corridor length calculated from (4.9) using boundary conditions (4.10–4.12) with  $\tilde{m} = 5$ . These analytical approximations compare favourably with simulations which include corridor birth (at  $2\tilde{m}$ ) and patch recovery ( $n = 6$ ) – the typical values encountered by *Eciton burchelli*. The simulation results are the average of 1000 runs for each length of corridor. The simulation probabilities for a given corridor length sum to more than 1 since a birth in the corridor could, for example, lead to one success and one death. It was never observed that a single colony entering the corridor gave rise to 2 successes.

(4.9) with boundary conditions

$$\begin{aligned}
 r_k(0, \cdot, \cdot) &= 1 \\
 r_k(\cdot, 0, \cdot) &= 0 \\
 r_k(\cdot, k+1, \cdot) &= 0.
 \end{aligned} \tag{4.12}$$

We shall be interested in the values of  $p_k(\tilde{m}, k, 0)$ ,  $q_k(\tilde{m}, k, 0)$  and  $r_k(\tilde{m}, k, 0)$  since  $(\tilde{m}, k, 0)$  is the state encountered by the colony when first entering the corridor, and it is these values which are the corridor outcome probabilities we desire. The system (4.9) with boundary conditions (4.10–4.12) is solved iteratively on a computer and for small values of  $\tilde{m}$  may be solved by hand. Table 4.1 illustrates the values of  $p$ ,  $q$  and  $r$  for various lengths of corridor  $k$  with  $\tilde{m} = 5$ . Also shown in this table is the comparison of this analytic approximation compared to the probabilities obtained by computer simulation (again based on that of chapter 2) which includes both patch recovery and corridor birth. As one can see, the approximation appears to be a good one.

### Corridor Outcome Probabilities – Wider Corridors

Should we wish to consider a corridor wider than 180 metres, the above modelling technique fails and a computer simulation is the only means by which to obtain the

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#### 4.3. A MARKOV CHAIN MODEL

corridor outcome probabilities.

### 4.3.3 Results of Markov Chain Model

#### No Catastrophes

Figure 4-7 shows how the introduction of a 180 metre-wide corridor influences metapopulation persistence when the reserve is not subject to a catastrophe. For nearby patches, a narrow corridor significantly lengthens the expected time to extinction, but for distant patches, such a corridor worsens persistence times. Notice in particular the qualitative similarity between this Markov Chain model and the simulation model (fig. 4-2).

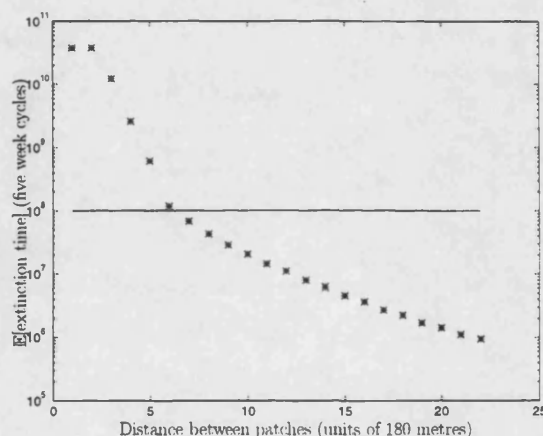


Figure 4-7: The expected time to metapopulation extinction under no catastrophe, according to equation (4.3), is plotted as a function of the distance between patches. Corridor length is measured in units of 180 metres and time in the usual five week activity cycles. As a comparison, the solution of the system with  $c = 0$ , i.e. no corridor, is given by the solid line. Notice that like the simulation model, the Markov Chain model predicts short narrow corridors are beneficial but longer ones are not necessarily so.

#### Type I Catastrophes

We shall restrict attention to a catastrophe occurring at rate  $k$ , killing colonies independently with probability  $\gamma \in [0, 1]$ . Thus  $p(i, j|n, m) = \tilde{p}(i|n)\tilde{p}(j|m)$  where  $\tilde{p}(i|n) = \binom{n}{i}\gamma^i(1-\gamma)^{n-i}$ . Figures 4-8–4-9 show some examples of how a 180 metre-wide corridor can alter persistence of two habitat pockets under different type I catastrophes. Notice

that under these disasters, the critical corridor length (or more precisely, the critical corridor outcome probabilities) are different; the corridor can have a higher death rate under a catastrophe and still be beneficial while without catastrophes such a corridor would be dire. This implies that corridors are most useful when the metapopulation is subjected to catastrophes and habitat patches are frequently forced extinct so that corridors encourage recolonisation. In all cases, the expected time to extinction equalled the variance suggesting extinction times were exponentially distributed.

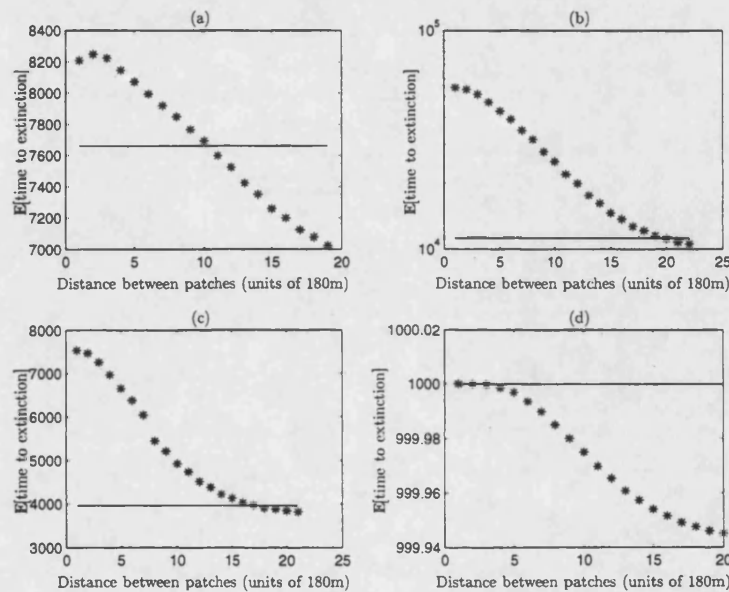


Figure 4-8: The expected time to extinction under a type I catastrophe occurring at rate  $k = 0.001$ . The impact of the catastrophe varies, deaths being distributed binomially with probability  $\gamma$ , (a)  $\gamma = 0.25$ , (b)  $\gamma = 0.5$ , (c)  $\gamma = 0.75$  and (d)  $\gamma = 1$ .

### Type II Catastrophes

As with type I catastrophes, attention is restricted to a deaths occurring with a binomial distribution so that  $p(i|n) = \binom{n}{i} \gamma^i (1 - \gamma)^{n-1}$  where  $\gamma$  is the probability a colony dies during a catastrophe. Furthermore, it is supposed the catastrophe occurs independently in the pockets at rate  $k_1 = k_2 = k$ .

Figures 4-10–4-11 show some examples of how a 180-metre wide corridor can alter the persistence of two habitat pockets under different type II catastrophes. Notice that

### 4.3. A MARKOV CHAIN MODEL

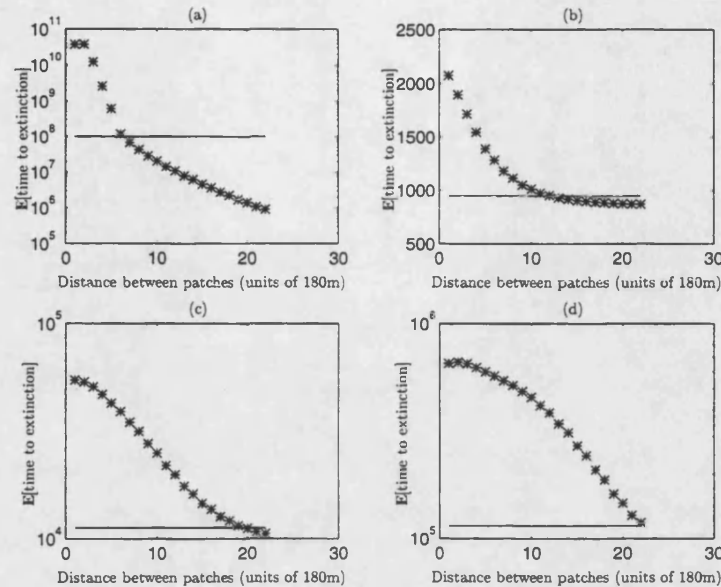


Figure 4-9: The expected time to extinction (five week activity cycles) for the dumbbell under a type I catastrophe occurring at rate  $k$  having deaths distributed binomially with mean  $\gamma = 0.5$ . In (a)  $k = 0$ , (b)  $k = 0.01$ , (c)  $k = 0.001$  and (d)  $k = 0.0001$ .

under these catastrophes the critical corridor length (or, more precisely, the critical corridor outcome probabilities) are different. That is to say a catastrophe greatly influences the effectiveness of a corridor in a metapopulation.

It was observed in all instances, by using the formula for the variance of the extinction times (4.4), that extinction times are exponentially distributed, since in all cases, the variance equalled the mean.

#### 4.3.4 Discussion of Markov Chain Model

The Markov Chain model has answered the major criticism of the simulation model; generality. It is a very general model, easily capable of dealing with exceptionally complicated population dynamics. While there are a few metapopulation models which can cope with non-linear birth and death rates (e.g. Mangel and Tier, 1993), many fewer can consider non-linear, i.e. density-dependent, dispersal. Many natural populations have density-dependent dispersal rates (Hanski et al., 1996; Saether et al., 1999), especially natal dispersal rates, and the ability of this model to deal with this important

#### 4.3. A MARKOV CHAIN MODEL

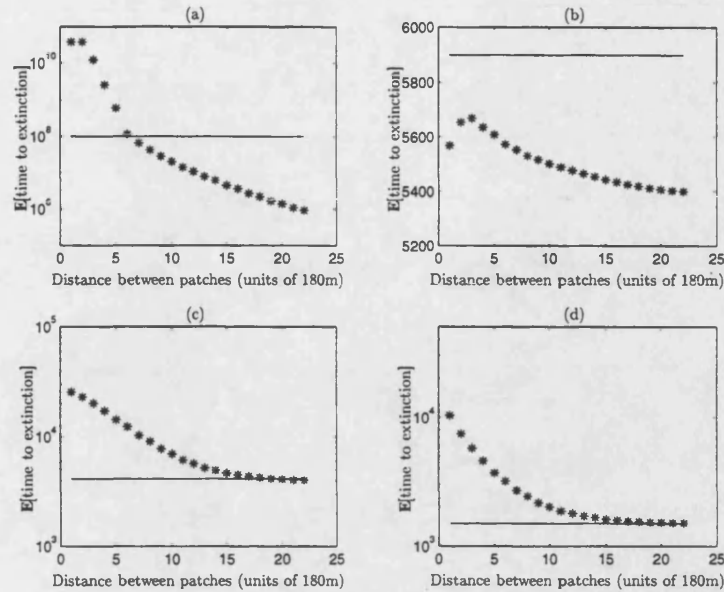


Figure 4-10: The expected time to reserve extinction under a type II catastrophe occurring at rate  $k = 0.001$ . The numbers dying in each catastrophe is binomially distributed with mean  $\gamma$ . (a)  $\gamma = 0$ , (b)  $\gamma = 0.5$ , (c)  $\gamma = 0.75$  and (d)  $\gamma = 1$ .

factor is its major strength.

One of the surprising results of the modelling is that under certain conditions (e.g. type II catastrophe,  $k = 0.001$ ,  $\gamma = 0.5$ , fig 4-10(b)), the inclusion of a narrow corridor always reduced persistence regardless of the distance between patches. Perhaps wider corridors, having higher entrance rates and success rates, could prolong persistence, although not necessarily; Quinn and Hastings (1987) give examples of populations who persist longer if they are fragmented than if they were connected. Whilst this initially sounds bizarre, it is in fact extremely simple, being based around how one carries eggs in baskets. Consider the two patch metapopulation of above supporting about eight colonies at the quasi-equilibrium. Suppose a complete catastrophe (i.e. kills all individuals with probability 1) effects the reserve, acting as a type I if the patches are joined, or a type II if they are separate (e.g. a disease might provide such a disaster). Thus the first time a catastrophe occurs, the connected reserve is forced extinct while the separated patches still support populations.

Especially pleasing to note is that the predictions of this model agree with the simu-

#### 4.3. A MARKOV CHAIN MODEL



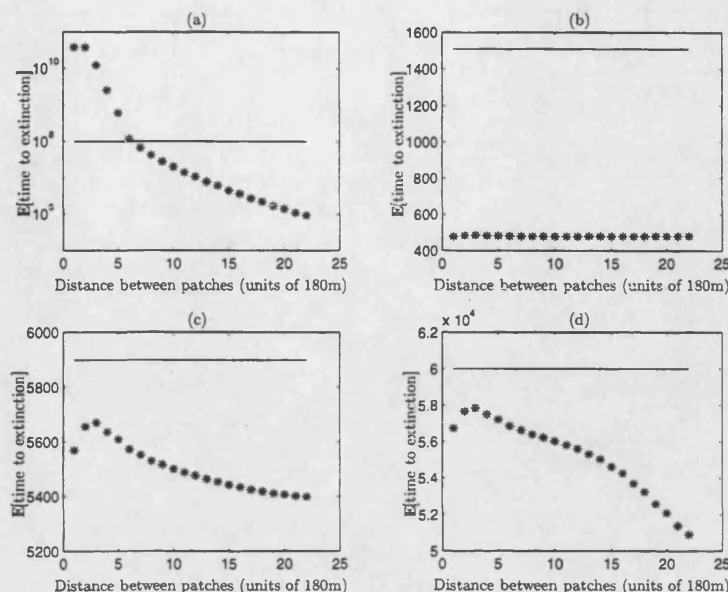


Figure 4-11: The expected time to dumbbell extinction under a type II catastrophe occurring at rate  $k$ . The numbers dying in each catastrophe is binomially distributed with mean  $\gamma = 0.5$ . (a)  $k = 0$ , (b)  $k = 0.01$ , (c)  $k = 0.001$  and (d)  $k = 0.0001$ .

lation in as far as certain corridors can reduce persistence. Though qualitatively similar to the simulation model, this Markov Chain model differed quantitatively, specifically through the exclusion of queen death, but also the slightly different movement rules between the models (i.e. the MC stepper versus the simulation jumper) has an effect. The inclusion of queen death is, however, relatively straightforward. For example, the equation (4.9) describing the probability of successfully passing through a corridor of length  $k$  would be rewritten as

$$\begin{aligned}
 p_k(\gamma, x, y) &= \frac{1}{2}(1 - \delta)p_k(\gamma - 1, x + 1, y + 1) \\
 &+ \begin{cases} (1 - \delta)\frac{1}{2}p_k(\gamma + 1, x - 1, 0) & \text{if } y = 0 \\ (1 - \delta)\frac{1}{2}p_k(\gamma - 1, x - 1, y - 1) & \text{otherwise} \end{cases} \quad (4.13)
 \end{aligned}$$

where  $\delta$  is the probability that the queen dies in a time step. Of course, the boundary conditions must then be adapted, and this is where the difficulties first arise. The effect of queen death is to increase the corridor death probability, making the corridor more

#### 4.3. A MARKOV CHAIN MODEL



of a demographic sink than it is shown to be above.

This modelling has shown not only that habitat corridors can reduce metapopulation persistence, but also describes the mechanism for this reduction. It is subsequently clear that wildlife corridors are beneficial only when they satisfy certain criteria, e.g. they have low mortality rates. Moreover, the precise impact of the corridor depends strongly on the presence and nature of any disaster which might befall the population. Catastrophes were seen to greatly influence conservation programs; for example, a corridor which is beneficial in the absence of catastrophes, may become a liability under one. This modelling has emphasised the importance of understanding disasters which might act on the populations – this is presently not given enough attention in the literature.

In order to obtain extinction times from this model, one has to solve a large system of linear equations; even with modern computers this can take a considerable amount of time. In the examples considered above, the pockets were reasonably small, but even so gave rise to system of approximately 1500 simultaneous equations. For larger pocket size, or, especially, for more than two pockets, the size of the system increases exponentially. Thus the Markov Chain model is impractical to use on large metapopulations. Furthermore, conservationists would be interested to know regions of  $pqr$  parameter space in which a corridor ought to lie; the Markov Chain model cannot explicitly do this.

## 4.4 A Stochastic Differential Equation Model

The simulation model and Markov Chain model were both seen to be very expensive and time-consuming models for practical use. They both required a great deal of computing power, be it for a simulation or to solve large systems of linear equations.

In this section a stochastic differential equation model is derived describing the approximate dynamics of a structured metapopulation. Properties of this system are then obtained from which an asymptotic expression for the expected time to reserve extinction is derived; this asymptotic expression taking the form of a single equation.

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### 4.4. A STOCHASTIC DIFFERENTIAL EQUATION MODEL

#### 4.4.1 Derivation of Model

Consider a reserve of  $n$  patches which allow the movement of individuals from a given patch to a subset of the other patches. We assume stochastic logistic population growth within each patch, patch  $i$  having carrying capacity  $K_i$  and intrinsic growth rate  $\rho_i$ ,  $i = 1 \dots n$ . The rate at which individuals leave patch  $i$  for patch  $j$  shall be denoted by  $c_{ij}$  (n.b. this is independent of population size within the patch – see later discussion) though not every individual will be successful. The probability an individual succeeds is given by  $p_{ij}$  and the probability it dies in the process of dispersal is given by  $r_{ij}$ . Note that  $p_{ij} + r_{ij} \leq 1$  since the individual can return to the original patch. Following in the manner of Nisbet and Gurney (1982) and van Herwaarden and Grasman (1995), we have the following transitions over a short interval of time  $\Delta t$ :

<i>Transition</i>	<i>Probability</i>	<i>Description</i>
$N_j \rightarrow N_j + 1$	$\rho_j N_j \Delta t$	Birth in patch $j$
$N_j \rightarrow N_j - 1$	$\rho_j N_j^2 \Delta t / K_j$	Death in patch $j$
	$\sum_{i=1, i \neq j}^n c_{ji} r_{ji} N_j \Delta t$	Dispersal death from patch $j$ to $i$
$N_i \rightarrow N_i + 1$	$c_{ji} p_{ji} N_j \Delta t$	Successfull dispersal from
$N_j \rightarrow N_j - 1$		patch $j$ to patch $i$

Notice that the per capita death term tends to zero as  $N_j \rightarrow 0$ . To be more realistic, we could have chosen the per capita death term to be  $(b + N_j/K_j)$  which tends to some non-zero constant  $b$  as  $N_j \rightarrow 0$ . For simplicity we have assumed  $b = 0$ . This assumption is unlikely to alter the conclusions of the modelling since much of the analysis occurs when  $N_j > 0$ .

The above transitions yield for the conditional first and second moments of the changes of  $N_i$  over the time interval  $\Delta t$ ,

$$\begin{aligned}\mathbb{E}[\Delta N_j] &= \rho_j N_j \Delta t - \rho_j \frac{N_j^2}{K_j} \Delta t - \sum_{i \neq j} c_{ji} r_{ji} N_j \Delta t - \sum_{i \neq j} c_{ji} p_{ji} N_j \Delta t \\ &\quad + \sum_{i \neq j} c_{ij} p_{ij} N_i \Delta t\end{aligned}\tag{4.14a}$$

$$\begin{aligned}\mathbb{E}[(\Delta N_j)^2] &= \rho_j N_j \Delta t + \rho_j \frac{N_j^2}{K_j} \Delta t + \sum_{i \neq j} c_{ji} r_{ji} N_j \Delta t + \sum_{i \neq j} c_{ji} p_{ji} N_j \Delta t \\ &\quad + \sum_{i \neq j} c_{ij} p_{ij} N_i \Delta t.\end{aligned}\tag{4.14b}$$

Working with such equations is cumbersome and so we make a variety of changes and simplifications. These changes serve only to ease the mathematics, they apply to numerous biological systems, including *Eciton burchelli* army ants. As before, the simplest example of a metapopulation is a two-patch reserve and hence we shall work with  $n = 2$ . Furthermore, for simplicity we assume  $c_{12} = c_{21} = c$ ,  $p_{12} = p_{21} = p$ ,  $r_{12} = r_{21} = r$  and  $\rho_1 = \rho_2 = \rho$ . We shall also assume that the two patches have the same carrying capacities  $K_1 = K_2 = K$ . Of course, all these assumptions can be relaxed, but without them it is difficult to obtain meaningful properties from the resulting stochastic differential equations.

Non-dimensionalise (4.14) by writing  $x_j = N_j/K$  to obtain

$$\begin{aligned}\mathbb{E}[\Delta x_1] &= \rho x_1 \Delta t - \rho x_1^2 \Delta t - c r x_1 \Delta t - c p x_1 \Delta t + c p x_2 \Delta t \\ \mathbb{E}[\Delta x_2] &= \rho x_2 \Delta t - \rho x_2^2 \Delta t - c r x_2 \Delta t - c p x_2 \Delta t + c p x_1 \Delta t \\ \mathbb{E}[(\Delta x_1)^2] &= \frac{\rho x_1}{K} \Delta t + \frac{\rho x_1^2}{K} \Delta t + \frac{c r x_1}{K} \Delta t + \frac{c p x_1}{K} \Delta t + \frac{c p x_2}{K} \Delta t \\ \mathbb{E}[(\Delta x_2)^2] &= \frac{\rho x_2}{K} \Delta t + \frac{\rho x_2^2}{K} \Delta t + \frac{c r x_2}{K} \Delta t + \frac{c p x_2}{K} \Delta t + \frac{c p x_1}{K} \Delta t.\end{aligned}$$

It is observed that the variances of  $\Delta x_1$  and  $\Delta x_2$  equal the second moments up to  $\mathcal{O}((\Delta t)^2)$ . Under the assumption of continuity, the stochastic jump process is thus

approximated by the system of stochastic differential equations of Ito type

$$\begin{aligned} dx_1 = & [\rho x_1(1 - x_1) - crx_1 - cp x_1 + cp x_2] dt + \sqrt{\frac{\rho x_1}{K}} dW_1 \\ & - \sqrt{\frac{\rho x_1^2}{K}} dW_2 - \sqrt{\frac{crx_1}{K}} dW_3 - \sqrt{\frac{cp x_1}{K}} dW_4 + \sqrt{\frac{cp x_2}{K}} dW_5 \end{aligned} \quad (4.15a)$$

$$\begin{aligned} dx_2 = & [\rho x_2(1 - x_2) - crx_2 - cp x_2 + cp x_1] dt + \sqrt{\frac{\rho x_2}{K}} dW_6 \\ & - \sqrt{\frac{\rho x_2^2}{K}} dW_7 - \sqrt{\frac{crx_2}{K}} dW_8 - \sqrt{\frac{cp x_2}{K}} dW_5 + \sqrt{\frac{cp x_1}{K}} dW_4 \end{aligned} \quad (4.15b)$$

with  $dW_i$  being the increments of the independent Wiener processes  $W_i(t)$ ,  $i = 1, \dots, 8$  (see, for example, Ludwig, 1975; Schuss, 1980). In the classic form (4.15) is written as

$$dx = b(x)dt + \sqrt{\epsilon}\sigma(x)dw \quad (4.16)$$

where  $\epsilon$  is defined to  $1/K$ , a measure of the stochasticity in the system.

From this equation the Fokker-Planck (or forward Kolmogorov) equation can be obtained, which is a partial differential equation for the probability density function  $p(x_1, x_2, t)$  of finding the system in state  $(x_1, x_2)$  at time  $t$ . It is

$$\frac{\partial p}{\partial t} = - \sum_{i=1}^2 \frac{\partial}{\partial x_i} (b_i p) + \frac{\epsilon}{2} \sum_{i,j=1}^2 \frac{\partial^2}{\partial x_i \partial x_j} (a_{ij} p) \quad (4.17)$$

where  $b$  denotes the drift in the system and  $a = \sigma\sigma^T$  is the diffusion matrix. Here  $\sigma^T$  denotes the transpose of the matrix  $\sigma$ . Thus for the stochastic differential equation (4.15) we have drift vector

$$b = \begin{pmatrix} \rho x_1(1 - x_1) - crx_1 - cp x_1 + cp x_2 \\ \rho x_2(1 - x_2) - crx_2 - cp x_2 + cp x_1 \end{pmatrix} \quad (4.18)$$

and diffusion matrix

$$a = \begin{pmatrix} \rho x_1(1+x_1) + cx_1 + cx_1 + cx_2 & -cp(x_1+x_2) \\ -cp(x_1+x_2) & \rho x_2(1+x_2) + cx_2 + cx_2 + cx_1 \end{pmatrix}. \quad (4.19)$$

Exact solutions of equations such as (4.17) are difficult to find, hence in the following section an asymptotic solution as  $\epsilon \rightarrow 0$  is derived.

#### 4.4.2 An Asymptotic Solution of the Fokker-Planck Equation

We seek a solution of (4.17) with left hand side equal to zero (i.e. at the quasi-steady state). A simple WKB-Ansatz to the solution of (4.17) is (Ludwig, 1975; Roozen, 1987; Grasman, 1996)

$$p(x_1, x_2) = C \exp \left\{ -\frac{Q(x_1, x_2)}{\epsilon} \right\} \quad (4.20)$$

where  $C$  is some normalising constant, since we demand

$$\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} p(x_1, x_2) dx_2 dx_1 = 1,$$

and  $Q$  is some as yet unknown (symmetric) function of  $x_1$  and  $x_2$ .

Substituting (4.20) into the Fokker-Planck equation (4.17) and collecting the leading order terms  $O(1/\epsilon)$  gives the Eikonal equation

$$0 = \sum_{i=1}^2 b_i \frac{\partial Q}{\partial x_i} + \frac{1}{2} \sum_{i,j=1}^2 a_{ij} \frac{\partial Q}{\partial x_i} \frac{\partial Q}{\partial x_j} \quad (4.21)$$

which is with  $\mathbf{b}$  and  $a$  as defined in (4.18) and (4.19) respectively,

$$\begin{aligned}
 0 = & [\rho x_1(1 - x_1) - crx_1 - cp x_1 + cp x_2] \frac{\partial Q}{\partial x_1} + [\rho x_2(1 - x_2) - crx_2 - cp x_2 + cp x_1] \frac{\partial Q}{\partial x_2} \\
 & + \frac{1}{2} [\rho x_1(1 + x_1) + crx_1 + cp x_1 + cp x_2] \left( \frac{\partial Q}{\partial x_1} \right)^2 - cp(x_1 + x_2) \frac{\partial Q}{\partial x_1} \frac{\partial Q}{\partial x_2} \\
 & + \frac{1}{2} [\rho x_2(1 + x_2) + crx_2 + cp x_2 + cp x_1] \left( \frac{\partial Q}{\partial x_2} \right)^2.
 \end{aligned} \tag{4.22}$$

We shall assume that (4.20) and (4.21) describe the stochastic system sufficiently well. Otherwise, higher order terms of  $\epsilon$  must be included in the approximation (see, for example, Ludwig, 1975).

#### Local Analysis near the Equilibrium

Most of the time the stochastic system as described above will be close to its deterministic equilibrium,  $\mathbf{x}^*$ , being the steady state of the dynamical system

$$\frac{d\mathbf{x}}{dt} = \begin{pmatrix} \rho x_1(1 - x_1) - crx_1 - cp x_1 + cp x_2 \\ \rho x_2(1 - x_2) - crx_2 - cp x_2 + cp x_1 \end{pmatrix} \equiv \mathbf{b}(\mathbf{x})$$

which is clearly seen to be

$$\begin{pmatrix} x_1^* \\ x_2^* \end{pmatrix} = \begin{pmatrix} \alpha \\ \alpha \end{pmatrix} \tag{4.23}$$

where  $\alpha = 1 - cr/\rho$ . Hence we shall seek a solution of equation (4.22) in a region around  $\mathbf{x}^* = (\alpha, \alpha)$ .

We approximate the stochastic system (4.15) close to  $(\alpha, \alpha)$  by its deterministic linearised system

$$\frac{d\bar{\mathbf{x}}}{dt} = \begin{pmatrix} -(\rho\alpha + cp) & cp \\ cp & -(\rho\alpha + cp) \end{pmatrix} \bar{\mathbf{x}} \equiv B\bar{\mathbf{x}} \tag{4.24}$$

where  $\bar{x}_i \equiv x_i - \alpha$  is a small perturbation from the quasi-equilibrium.

An important observation is that the matrix  $B$  defined above satisfies

$$B_{ij} = \left. \frac{\partial b_i}{\partial x_j} \right|_{(\alpha, \alpha)}$$

where  $b_i$  is the  $i$ th entry of the drift vector defined in equation (4.18). Notice also from (4.24), that close to the quasi-equilibrium  $(\alpha, \alpha)$ , we can approximate the drift vector as

$$b_i \approx \sum_{j=1}^2 B_{ij} \bar{x}_j \quad i = 1, 2. \quad (4.25)$$

Recall the stochastic terms in SDEs are normally distributed with mean zero. This suggests that the stochastic system described by (4.16) spends the majority of its time close to the point where the stochastic terms are zero, i.e. the deterministic equilibrium, and moreover, that the distribution around the quasi-equilibrium could also be normal. Hence we shall seek a function  $Q$  which, close to the quasi-equilibrium, is approximated by  $\tilde{Q}$  where

$$\tilde{Q}(x_1, x_2) = \sum_{i,j=1}^2 \frac{1}{2} P_{ij} \bar{x}_i \bar{x}_j. \quad (4.26)$$

Here  $P$  denotes a 2-by-2 symmetric matrix. Notice that upon substituting  $\tilde{Q}$  into (4.20), the probability distribution function is 2-variate normal. Differentiating  $\tilde{Q}$  with respect to  $x_i$  yields

$$\frac{\partial \tilde{Q}}{\partial x_i} = \sum_{j=1}^2 P_{ij} \bar{x}_j. \quad (4.27)$$

Now substituting the approximations (4.25) and (4.27) into (4.22) yields

$$0 = \sum_{i=1}^2 \left( \sum_{j=1}^2 B_{ij} \bar{x}_j \right) \left( \sum_{j=1}^2 P_{ij} \bar{x}_j \right) + \frac{1}{2} \sum_{i,j=1}^2 a_{ij} \left( \sum_{k=1}^2 P_{ik} \bar{x}_k \right) \left( \sum_{k=1}^2 P_{jk} \bar{x}_k \right). \quad (4.28)$$

(Recall  $a_{ij}$  is the diffusion matrix as defined in (4.19) which here is evaluated at  $(\alpha, \alpha)$ .)

Collecting the terms in (4.28) in the form

$$\begin{pmatrix} \bar{x}_1 \bar{x}_1 & \bar{x}_1 \bar{x}_2 \\ \bar{x}_2 \bar{x}_1 & \bar{x}_2 \bar{x}_2 \end{pmatrix}$$

and using the symmetry of  $P$ , (4.28) yields the matrix equation

$$PAP + PB + B^T P = 0. \quad (4.29)$$

See also Cohen and Lewis (1967), Ludwig (1975), Roozen (1987), Roozen (1989) and Grasman (1996). Assuming  $P$  is non-singular, pre and post-multiply (4.29) by  $S = P^{-1}$  to obtain

$$A + BS + SB^T = 0. \quad (4.30)$$

Substituting for  $A$  and  $B$  into (4.30) and rewriting  $S$  by stacking its columns yields the linear system of equations

$$\alpha \begin{pmatrix} -\rho(1+\alpha)-cr-2cp \\ 2cp \\ 2cp \\ -\rho(1+\alpha)-cr-2cp \end{pmatrix} = \begin{pmatrix} -2(\rho\alpha+cp) & cp & cp & 0 \\ cp & -2(\rho\alpha+cp) & 0 & cp \\ cp & 0 & -2(\rho\alpha+cp) & cp \\ 0 & cp & cp & -2(\rho\alpha+cp) \end{pmatrix} \begin{pmatrix} s_{11} \\ s_{21} \\ s_{12} \\ s_{22} \end{pmatrix}. \quad (4.31)$$

Solving this system gives  $S$  as

$$S = \frac{\alpha}{2[(\rho\alpha + cp)^2 - (cp)^2]} \times \begin{pmatrix} \rho(1+\alpha)(\rho\alpha+cp)+cr(\rho\alpha+cp)+2cp(\rho\alpha+cp)-2(cp)^2 & \rho(1+\alpha)cp+(cp)(cr)+2(cp)^2-2cp(\rho\alpha+cp) \\ \rho(1+\alpha)cp+(cp)(cr)+2(cp)^2-2cp(\rho\alpha+cp) & \rho(1+\alpha)(\rho\alpha+cp)+cr(\rho\alpha+cp)+2cp(\rho\alpha+cp)-2(cp)^2 \end{pmatrix}$$



and upon inverting  $S$  yields  $P$  to be

$$P = \frac{2}{\alpha \left\{ [\rho(1+\alpha) + c\tau + 2cp]^2 - 4(cp)^2 \right\}} \times \begin{pmatrix} (\rho\alpha + cp)[\rho(1+\alpha) + c\tau + 2cp] - 2(cp)^2 & -(cp)[\rho(1+\alpha) + c\tau + 2cp] + 2cp(\rho\alpha + cp) \\ -(cp)[\rho(1+\alpha) + c\tau + 2cp] + 2cp(\rho\alpha + cp) & (\rho\alpha + cp)[\rho(1+\alpha) + c\tau + 2cp] - 2(cp)^2 \end{pmatrix}. \quad (4.32)$$

Substituting (4.32) into (4.26) gives an approximation for the function  $Q$

$$Q(x_1, x_2) = \frac{1}{2}P_1x_1^2 + P_2x_1x_2 + \frac{1}{2}P_1x_2^2 - \alpha(P_1 + P_2)x_1 - \alpha(P_1 + P_2)x_2 + \alpha^2(P_1 + P_2) \quad (4.33)$$

where  $P_1$  and  $P_2$  denote the diagonal and off-diagonal terms, respectively of the matrix  $P$  given in (4.32). Then substituting (4.33) into the WKB-Ansatz yields the probability density function as

$$p(x_1, x_2) = C \exp \left\{ -\frac{Q(x_1, x_2)}{\epsilon} \right\}.$$

#### 4.4.3 An Asymptotic Approximation for the Expected Extinction Time

##### Confidence Regions

An approximation for the probability distribution function has been derived above and from this function confidence regions for the system described by (4.15) can be constructed. Recall, the quasi-stationary probability density function is described by the WKB-Ansatz

$$p(x_1, x_2) = C \exp \{ -Q(x_1, x_2)/\epsilon \} \quad (4.34)$$

where  $Q$  is given in (4.33),  $\epsilon = 1/K$ , where  $K$  is the carrying capacity of the pockets, and  $C$  is a normalising constant. It is clear from this Ansatz that contours of constant  $Q$  in the state space are contours of constant probability. So let  $Q_z$  denote the value

of  $Q$  corresponding to the contour for which the probability of being in the region  $R$  enclosed by this contour is equal to  $z$ :

$$\int_R p(\mathbf{x}) d\mathbf{x} = z, \quad 0 \leq z \leq 1. \quad (4.35)$$

In order to construct the contour enclosing the confidence region of probability  $z$ , the corresponding value  $Q_z$  of  $Q$  must be determined. As in Roozen (1987), the following heuristic method is used. According to the local analysis, in a first approximation  $p$  has a 2-variate normal distribution around the equilibrium point  $(\alpha, \alpha)$  given by (4.34). By a standard result in probability theory,  $2Q(x)/\epsilon$  has a chi-square distribution with 2 degrees of freedom. The value  $2Q_z/\epsilon$  which will not be exceeded by  $2Q(x)/\epsilon$  with probability  $z$  can be found in a table of the chi-square distribution with 2 degrees of freedom. Indeed, for 2 degrees of freedom, it can be derived that (e.g. Roozen, 1987)

$$Q_z = -\epsilon \ln(1 - z). \quad (4.36)$$

Hence, upon choosing the probability  $z$ , the corresponding value of  $Q$ ,  $Q_z$ , is given by (4.36) and upon substituting into the equation  $Q(x_1, x_2) = Q_z$  yields the confidence region to be

$$0 = \frac{1}{2}P_1x_1^2 + P_2x_1x_2 + \frac{1}{2}P_1x_2^2 - \alpha(P_1 + P_2)x_1 - \alpha(P_1 + P_2)x_2 + \alpha^2(P_1 + P_2) - Q_z. \quad (4.37)$$

By the examining the discriminant of this second degree equation, the confidence regions are seen to be ellipses. Thus, rotating the system  $(x_1, x_2)$  anticlockwise by  $\pi/4$  to the  $(x', y')$  system, and rearranging (4.37) yields

$$1 = \frac{(x' - \sqrt{2}\alpha)^2}{\xi_1^2} + \frac{(y')^2}{\xi_2^2} \quad (4.38)$$

with

$$\begin{aligned}\xi_1 &= \left( \frac{XQ_z}{\rho Y} \right)^{1/2} \\ \xi_2 &= \left( \frac{\alpha XQ_z}{Z} \right)^{1/2} \\ X &= [\rho(1+\alpha) + cr + 2cp]^2 - 4(cp)^2 \\ Y &= \rho(1+\alpha) + cr + 4cp \\ Z &= (\rho\alpha + cp)(\rho(1+\alpha) + cr).\end{aligned}$$

It is now clear that the confidence regions are ellipses centred at  $(x_1, x_2) = (\alpha, \alpha)$ , the deterministic steady state, and have semi-major and semi-minor axes as described by the constants  $\xi_1$  and  $\xi_2$  (see figure 4-12).

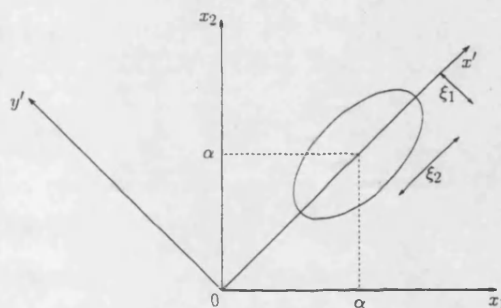


Figure 4-12: The confidence regions of the stochastic system (4.15) are ellipses centred at the deterministic equilibrium  $(\alpha, \alpha)$ . The semi-major and semi-minor axes depend on the corridor parameters. It can be observed that upon reducing the probability of corridor death,  $r$ , the ellipses shrink. This suggests that large deviations away from the quasi-equilibrium are minimised by reducing  $r$ , i.e. metapopulation persistence is prolonged by minimising  $r$ .

#### Expected Time for Single Reserve Extinction

Metapopulation extinction is caused by a large deviation from the quasi-equilibria (see, for example, Ellis, 1985) and the most likely route to metapopulation extinction is for one of the patches to go extinct followed by the other. Hence, an approximation of the expected time for just one of the patches to go extinct is of interest. In the following

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#### 4.4. A STOCHASTIC DIFFERENTIAL EQUATION MODEL

calculations, it is assumed that the local analysis used above is valid far from the equilibrium. In cases when this assumption is not valid, higher order solutions of the Fokker-Planck equation (4.17) are required.

Suppose one of the patches, say patch 2, is extinct, i.e.  $x_2 = 0$ . The most likely state for the population of patch 1 can be found from the confidence regions; it is the point at which the confidence region just touches the  $x_2 = 0$  axis. Let  $C_2$  denote the value of  $Q_z$  in (4.37) for which this occurs. It is then seen that upon setting  $x_2 = 0$  in (4.37),

$$\begin{aligned} C_2 &= \frac{\alpha^2(P_1 + P_2)}{2} \left(1 - \frac{P_2}{P_1}\right) \\ &= \rho\alpha^3 \left( \frac{\rho(1+\alpha)+cr+4cp}{[\rho(1+\alpha)+cr+2cp]^2 - 4(cp)^2} \right) \left( \frac{(\rho\alpha+2cp)(\rho(1+\alpha)+cr)}{(\rho\alpha+cp)[\rho(1+\alpha)+cr+2cp]-2(cp)^2} \right) \end{aligned} \quad (4.39)$$

and the most probable state for  $x_1$  to be in is thus

$$\hat{x} = \alpha \frac{P_1 + P_2}{P_1} = \alpha \left\{ 1 + (cp) \left( \frac{\rho(1+\alpha) - cr}{[\rho(1+\alpha) + cr + 2cp]^2 - 2(cp)^2} \right) \right\} < \alpha. \quad (4.40)$$

Furthermore, Ludwig (1975) shows in the asymptotic analysis for small  $\epsilon$ , that the expected exit time for the stochastic system is given by

$$T \approx \exp(Q(\hat{x})/\epsilon)$$

where  $\hat{x}$  is the boundary point at which  $Q$  takes its minimal value at the boundary. That is to say, the most probable point of exit is the boundary state  $\hat{x} = (\hat{x}, 0)$ , so that the expected time for one patch to go extinct is

$$\tilde{T} \approx \exp(C_2/\epsilon), \quad \text{as } \epsilon \rightarrow 0. \quad (4.41)$$

#### 4 State Model to Calculate Dumbbell Persistence Times

It remains to derive an expression for the expected extinction time for a two-patch metapopulation. From the previous analysis, this is a relatively straightforward task.

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#### 4.4. A STOCHASTIC DIFFERENTIAL EQUATION MODEL

We approximate the stochastic system as described by (4.15) to be a four state model, see figure 4-13. One of the states, state 3, corresponds to the quasi-equilibrium  $(\alpha, \alpha)$ . Two of the states (states 1 and 2) correspond to one patch being extinct and the other occupied at the population level described in (4.40) while the fourth state, state 0, corresponds to metapopulation extinction.

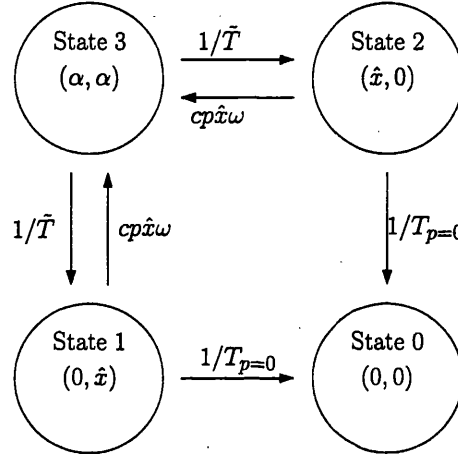


Figure 4-13: The approximate four state model for the system of stochastic differential equations in (4.15). State 3 corresponds to the deterministic equilibrium  $(\alpha, \alpha)$ , state 2 and 1 correspond to one patch extinction  $(\hat{x}, 0)$  and  $(0, \hat{x})$  respectively and state 0 corresponds to metapopulation extinction. State 0 in this Markov Chain is, of course, absorbing.

The system evolves according to certain transition probabilities. The rate at which the system leaves state 3 to state 1 or 2 is known from the above analysis – it is simply the reciprocal of the expected patch extinction time in (4.41). The rate at which the system returns from states 1 and 2 to state 3 is simply the rate at which colonisers leave a patch and successfully reach and restart the population in the other patch. From the initial assumptions, the rate at which successful colonisers arrive at one patch is  $cp\bar{x}$  where  $\bar{x}$  denotes the population in the dispersal population,  $c$  the corridor entrance rate and  $p$  the probability of successful passage. This rate must then be multiplied by the probability  $\omega$  that a single coloniser will restart the population. Finally, there is a possibility of moving from states 1 and 2 to state 0 – i.e. to metapopulation extinction. This rate is simply the reciprocal of the expected lifetime of a single population.

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#### 4.4. A STOCHASTIC DIFFERENTIAL EQUATION MODEL

This can be easily derived from the above analysis upon putting  $p = 0$  in (4.39) and substituting into (4.41) to get

$$T_{p=0} = \exp\left(\frac{C_{p=0}}{\epsilon}\right) \quad \epsilon \rightarrow 0$$

as the expected time to extinction for a single occupied patch.

Thus a Markov chain model can be constructed for the four state system and the expected time for metapopulation extinction can be calculated. Let  $T(i)$  be the expected time to move from state  $i$  to state 0 – i.e. extinction. Then, in a similar argument to models seen previously, we have the following system of equations where  $\Delta t$  is a small time increment

$$\begin{aligned} T(0) &= 0 \\ T(1) &= \Delta t + (1/T_{p=0})\Delta t T(0) + cp\hat{x}\omega\Delta t T(3) \\ &\quad + (1 - (1/T_{p=0})\Delta t - cp\hat{x}\omega\Delta t)T(1) + \mathcal{O}(\Delta t) \\ T(2) &= \Delta t + (1/T_{p=0})\Delta t T(0) + cp\hat{x}\omega\Delta t T(3) \\ &\quad + (1 - (1/T_{p=0})\Delta t - cp\hat{x}\omega\Delta t)T(2) + \mathcal{O}(\Delta t) \\ T(3) &= \Delta t + (1/\tilde{T})\Delta t T(2) + (1/\tilde{T})\Delta t T(1) + (1 - (2/\tilde{T})\Delta t)T(3) + \mathcal{O}(\Delta t) \end{aligned}$$

Dividing each equation by  $\Delta t$ , letting  $\Delta t \rightarrow 0$  and using symmetry ( $T(1) = T(2)$ ) gives two simultaneous equations whose solutions are

$$\begin{aligned} T(1) &= T(3) - \frac{\tilde{T}}{2} \\ T(3) &= T_{p=0} \left[ 1 + \left( cp\hat{x}\omega + \frac{1}{T_{p=0}} \right) \frac{\tilde{T}}{2} \right]. \end{aligned}$$

Thus the expected time to metapopulation extinction from the quasi-steady state  $(\alpha, \alpha)$  is given by

$$T = \exp\left(\frac{\alpha^3}{2\epsilon}\right) \left[ 1 + \frac{1}{2} \left( cp\hat{x}\omega + \exp\left(\frac{-\alpha^3}{2\epsilon}\right) \right) \exp\left(\frac{C_2}{\epsilon}\right) \right] \quad (4.42)$$

where  $\hat{x}$  is as defined in (4.40) and  $C_2$  is defined in (4.39).

#### 4.4.4 Results of SDE Model

##### Extinction Time as a Function of Outcome Probabilities

One of the criticisms of the Markov Chain model of section 4.3 was that it could not easily identify regions of  $pqr$  parameter space in which a corridor ought to lie to prolong persistence. With the SDE model this is now trivial since a vast range of  $p$  and  $r$  can be easily considered (figure 4-14).

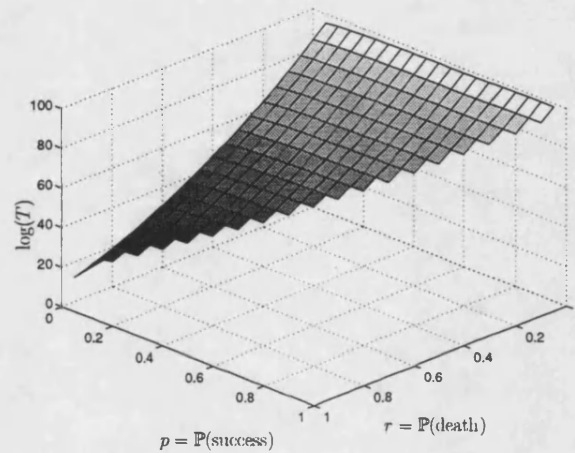


Figure 4-14: The extinction times of equation (4.42) are plotted for a range of corridor outcome probabilities with other variables being fixed,  $c = 0.01$ ,  $\rho = 1$ ,  $\epsilon = 0.01$ ,  $\omega = 1$ . The expected time to dumbbell extinction without a corridor,  $T_{c=0}$ , is found from equation (4.42) upon setting  $c = 0$ . In this example  $\log(T_{c=0}) = 50.4$ .

It is clear from fig. 4-14 that to prolong persistence, a corridor must have a low probability of death and a not too small probability of success.

##### Extinction Time as a Function of Corridor Entrance Rate

In Florida there are numerous examples of corridors connecting two patches of otherwise isolated natural habitat. However these corridors are not always continuous – many are intercepted by wide multi-lane highways (Mann, 1995; Mann and Plummer, 1995). A rodent, for example, will find this a formidable obstacle to navigate and the road will

surely cause significantly more mortality than a slight deterioration in habitat quality which may occur in the corridor. In this example, corridor width probably has little influence over the corridor outcome probabilities, and so it is worth examining how varying corridor width (i.e. corridor entrance rate) affects metapopulation persistence for fixed corridor outcome probabilities. An example is shown in figure 4-15.

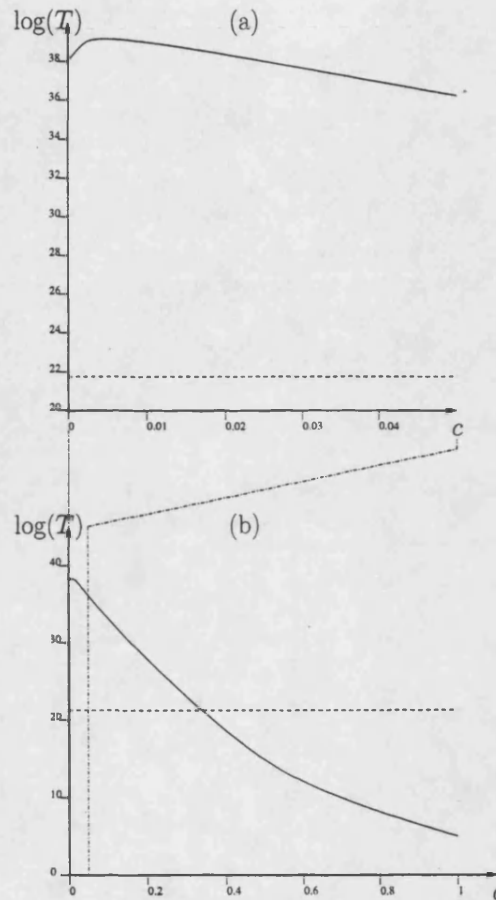


Figure 4-15: The expected time to dumbbell extinction is plotted as a function of corridor entrance rate  $c$  with fixed outcome probabilities. Here  $\rho = 1, p = 0.1, r = 0.7, \epsilon = 0.01$  and  $\omega = 1$ . The dashed line denotes the time to extinction in the absence of a corridor. (a) shows a magnification of (b) for very small values of  $c$ . Notice firstly that corridors with large  $c$  can reduce persistence times. Also notice that there appears to be an optimal value for  $c$ , or said differently, there appears to be an optimal corridor width. This last point of note may not be true in general as corridor width will effect the outcome probabilities.

It is suggested in figure 4-15(a) that there may exist an optimal corridor entrance

#### 4.4. A STOCHASTIC DIFFERENTIAL EQUATION MODEL



rate or width. The initial extension of the persistence time with increasing  $c$  shows the advantage of the corridor and its ability to send recolonisers to an empty patch. However, when the corridor entrance rate increases further, the numbers of individuals dying in the corridor becomes significant and it starts to act as the demographic sink seen previously. Of course, there will exist a relationship between the width of a corridor (and hence its entrance rate) and its outcome probabilities, so that this particular finding is somewhat debatable, but it serves to highlight the importance of corridor death on metapopulation persistence.

#### **Extinction Time as a Function of $\epsilon$**

Clearly the size of the habitat patches will play an important role in determining metapopulation extinctions. This is accounted for in the model by the parameter  $\epsilon = 1/K$  where, recall,  $K$  is a typical population size in each patch. Figure 4-16 shows how the value of  $\epsilon$  influences the expected metapopulation extinction time for a corridor of fixed size. It is clear from this graph that persistence is always maximised when  $\epsilon$  is minimised, i.e. the patches are as large as possible. Notice also, that if the patches are reasonably small, so that  $\epsilon \approx 0.08$  in fig. 4-16, then the existence of a connecting corridor may not necessarily prevent extinctions.

#### **Extinction Time as a Function of Intrinsic Growth Rate $\rho$**

Conservation programmes can improve the quality of an environment. We have previously considered this within the corridor, but it may not always be possible to improve the quality of a corridor beyond a certain point. It may be possible, however, to improve the environment within a patch, i.e. alter either the carrying capacity of each patch, or the population's growth rate in it. Above we saw how the first of these effected metapopulation extinction; here we shall consider how the intrinsic growth rate  $\rho$  influences persistence.

Figure 4-17 shows how changing  $\rho$  alters the expected time to metapopulation extinction for a fixed corridor. Notice firstly that increasing  $\rho$  always lengthens the

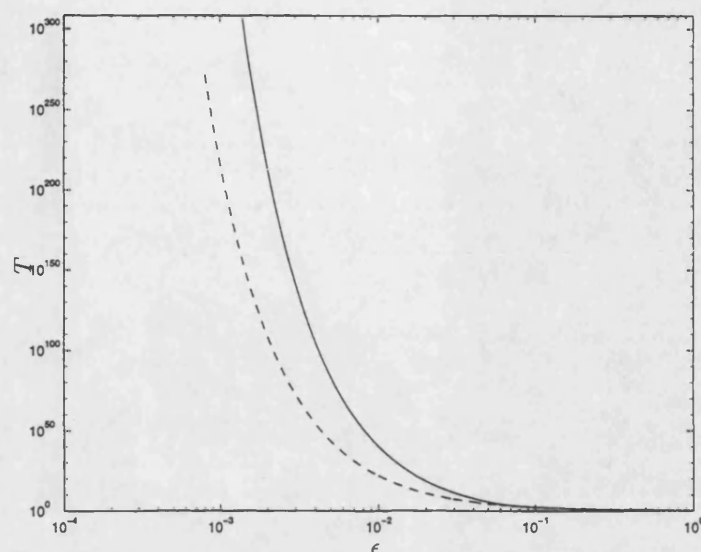


Figure 4-16: The expected time to dumbbell extinction (solid line) is plotted as a function of  $\epsilon$  from equation (4.42) with other parameters being  $c = 0.01, p = 0.2, r = 0.6, \omega = 1$  and  $\rho = 5$ . The expected time to extinction without a corridor joining the two patches is shown by the dashed line. It is not clear from the graph, but these lines intersect close to  $\epsilon = 0.08$  implying that when the patch size is small, this corridor is deleterious to persistence.

expected time to extinction, but it is most significant for small  $\rho$ . Furthermore, it is seen from figure 4-17 that a previously bad corridor can be transformed into a beneficial one simply by increasing  $\rho$ . This could have tremendous conservation implications.

#### Extinction Time as a Function of $\omega$

The probability that a single coloniser restarts a population in an empty patch has a large impact on the expected time to extinction (fig. 4-18). Notice that for small  $\omega$  small, a tiny increase will prolong metapopulation persistence by several orders of magnitude. Mechanisms for increasing  $\omega$  may include improving the quality of the environment which have been mentioned above and shall be discussed later.

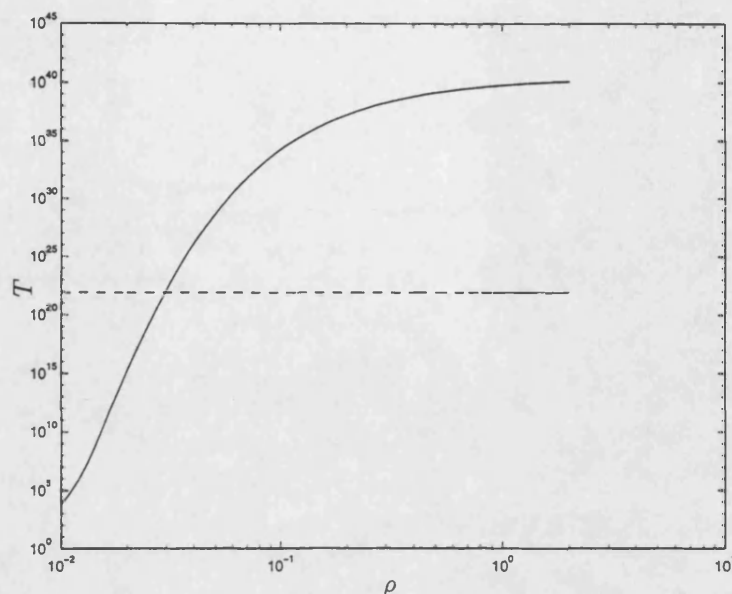


Figure 4-17: The expected time to dumbbell extinction is plotted as a function of the intrinsic growth rate  $\rho$  from equation (4.42) with  $c = 0.01, p = 0.2, r = 0.6, \epsilon = 0.01$  and  $\omega = 1$  (solid line). As a comparison, the expected time to extinction without a corridor is also shown (dashed line). Notice in this example that as  $\rho$  increases from 0, a bad corridor can be transformed into a good one and persistence can be increased by many orders of magnitude.

#### 4.4.5 Discussion of Stochastic Differential Equation Model

This third model of habitat corridors confirms the predictions of both the simulation model and the Markov Chain model. It shows that habitat corridors need not always prolong metapopulation persistence, they can considerably reduce it. However, like the previous models, corridors can be made to work by somehow improving the quality of the environment, this time either by improving the quality of the habitat within the corridor *or* improving the habitat patches. Whilst these conclusions were common to the previous models, quantification of them remained tricky – the SDE model, giving rise to a single equation, simplifies this aspect considerably.

There are several limitations of the SDE model, in particular the assumption that the corridor entrance rate is density-independent. While this assumption is probably valid for *Eciton burchelli* army ants, it remains dubious for many other animals (but

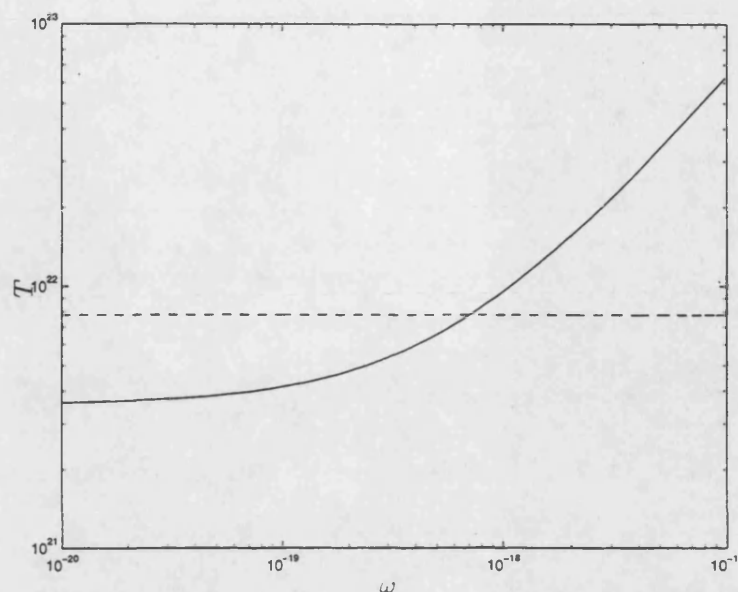


Figure 4-18: The expected time to dumbbell extinction is plotted as a function of the probability a single disperser can restart a patch population with  $c = 0.01$ ,  $p = 0.2$ ,  $r = 0.6$ ,  $\epsilon = 0.01$  and  $\rho = 1$  (solid line). The dashed line is the expected time to extinction in the absence of a corridor. Notice that for small  $\omega$ , a small increase improves persistence by several orders of magnitude.

see Saether et al., 1999, who states that adult dispersal rate in most species is density-independent, but natal dispersal is not necessarily so).

The expected time to dumbbell extinction was derived from a solution of the Fokker-Planck equation and then using classic asymptotic results, rather than solving the Dynkin equation as is typically done in such studies. The reason for this unusual, but not unique approach (see, e.g., Ludwig, 1975; Roozen, 1989), stems from difficulties in the boundary conditions. Recall the Dynkin equation is a PDE whose solution, under suitable boundary conditions, yields the expected time to extinction of a stochastic system. Typically these boundary conditions take the value zero on the axes, but in the metapopulation system they will be non-zero except at the origin when the metapopulation is extinct. Specifying the boundary data proved difficult, hence the use of the four-state approximation in section 4.4.3. A further advantage of this approach is that the solution of the Fokker-Planck equation, i.e. population numbers and distributions,

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#### 4.4. A STOCHASTIC DIFFERENTIAL EQUATION MODEL

is testable in the field, whilst the expected time to extinction, from solving the Dynkin equation, is not so easily testable.

## 4.5 Summary

In this chapter I have discussed the principles behind conservation corridors and why they have been widely used as conservation tools. Empirical studies into wildlife corridors were discussed, with the conclusion that the majority of studies fail to show whether corridors extend metapopulation persistence. A previous, verbal, argument that corridors could reduce persistence was stated and, via three different models, I have shown that this is indeed a possibility. The argument centred around a corridor acting as a demographic sink; the higher death rate may occur through a variety of causes. A spatially realistic computer simulation was developed for the army ant *Eciton burchelli* and it was discovered that, through habitat degradation by the ant colonies, certain corridors would reduce persistence; widening the corridor lessened this effect so that a bad corridor could be transformed into a good one. A Markov Chain model was subsequently developed for populations with unspecified birth and death processes and density-dependent dispersal; the mechanisms for corridor death were unspecified. It was discovered through applying parameters for the army ant *Eciton burchelli* that this model was qualitatively similar to the simulation model and shared common conclusions. Finally a stochastic differential equation model was derived where birth and death occurred via a logistic process and corridor entrance was now density-independent. This model had the same characteristics as the two previous ones with the advantage of being easier to use. Furthermore, the models each showed various mechanisms for turning a bad corridor into a good corridor – ranging from widening a corridor, improving the habitat quality within the corridor to changing the conditions in the patches if corridor alteration is not possible.

Empirical testing of these models must be high priority for they suggest that despite

the right intentions, conservation corridors may be very inappropriately named.

## Chapter 5

# The Antbirds

In earlier chapters, the importance of *Eciton burchelli* army ants on the tropical rain forest ecosystem was emphasised. In particular, it was mentioned that the existence of antbirds was entirely dependent upon the swarm-raiding army ants. This chapter is devoted to the antbirds; a colourful and noisy collection of birds who are often found perching just a few centimetres above army ant swarms. Antbirds are a crucial component of the rain forest ecosystem by controlling the insect population in the forest, not by directly competing with the army ants, but feeding off the fleeing insects and arthropods. It is commonly stated (e.g. Willis and Oniki, 1978) that without antbirds the insect and arthropod levels could escalate to extremely high densities causing untold disruption to this fragile ecosystem.

Antbirds have been extensively studied in the field, in particular on Barro Colorado Island (BCI), in the middle of Gatun Lake, Panama (Fig. 1-1). On this island, the antbird populations are undergoing some unusual changes, despite more-or-less constant environmental conditions. Certain antbirds, which are common in the nearby mainland forests, have been forced extinct on BCI, others are heading towards extinction, whilst a few have not changed in abundance over the last eighty years. Since antbirds, like many tropical bird species, are very poor dispersers, an island in a lake is no different to a forest fragment surrounded by hostile terrain; it is thus clearly important to understand the causes of the BCI extinctions because these issues relate to

Amazonia as a whole.

In section 5.1 a brief description of the biology of antbirds is given, especially the bicolored, spotted and ocellated antbirds. Particularly emphasised is the unusual, though by no means unique, territorial behaviour they exhibit. A popular, though untested, conjecture explaining the antbird extinctions on BCI is then stated which centres around predation levels on the island. In section 5.2 a simple heuristic discrete-time deterministic model is derived to test this hypothesis. After some analysis of the model, the hypothesis is seen to hold. The simple model has numerous limitations as is discussed in this section, and is subsequently replaced in section 5.3 by an discrete-time energy-based mechanistic model. This model explicitly includes competition and antbird interactions, something the simpler model failed to account for. Typical behaviours of this model are discussed and it is seen that this model also supports the conjecture explaining antbird extinctions. Finally, in section 5.4, the mechanistic model is used to explain how the territorial behaviour (or site-related dominance) exhibited by antbirds may have evolved from a heavily defended exclusive territory which is achieved by comparing how two rival strategies compare against one another.

## 5.1 Antbird Natural History

Upon observing a raid of swarming army ants, one will invariably witness the antbirds. They perch on branches a few centimetres above the raid front and every few minutes swoop down to capture a prey item. The prey items are not the army ants themselves, but the insects and arthropods disturbed and flushed out by the ants' raiding. In fact, over the course of a single day, the ant-following birds at a raid have been observed to obtain about 30 000 prey items between them – as much food as the ant colony itself (Willis and Oniki, 1978).

The antbirds, of which 238 different species have been identified (Willis and Oniki, 1978), have an amazing behavioural ecology. The most studied are the spotted antbird *Hylophylax naeviodes*, the bicolored antbird *Gymnopithys bicolor* and the ocellated antbird *Phaenostictus mcleannani*, the pioneering studies undertaken by Edwin Willis



during the 1960s and 1970s on Barro Colorado Island, Panama.

Antbirds live entirely within the tropical forests never venturing out of the shade – not even for a few metres – unless following an ant swarm (Stouffer and Bierregaard, 1995). Thus, because of the ant's reluctance to leave shelter, an isolated forest fragment is no different from an island surrounded by water. Indeed, Barro Colorado Island is about 500m from the mainland but no antbird has been known to cross this gap. This limited power of dispersal is not unusual, Diamond (as mentioned in Willis, 1974) found most forest birds, even strongly flying ones, absent on a forested island only 55m off the coast of New Guinea.

Young antbirds are reared in the months from April through to December, each brood taking about 13 weeks to complete development (Willis, 1974). A brood typically consists of two young, one male and one female. Although it is possible to raise three broods per year, high nest predation, especially on Barro Colorado Island, results in, on average, only one nesting per year producing young across all species. When young birds are present in the parental nest, the parents alternate between foraging and guarding the nest. Once the young birds leave the parental nest they become nomadic, wandering around the forest initially in search of ant raids from which to forage and later for potential mates. Different species of antbirds are able to forage away from ant swarms with varying degrees of success, thus allowing coexistence of competitors (Tilman, 1994). Across all species, females will generally pair after six months, i.e. in time for their first breeding season. Males, however, must wait a while longer since juvenile female mortality is higher than juvenile male mortality and therefore there is more competition for females (Willis, 1974). Indeed, despite an even birth ratio, adult bicolor males outnumber bicolor females roughly 1.7 to 1 (Willis, 1967). Once a pair bond forms, the birds establish a nest site and a territory. This territory is not exclusive as the birds practice, to varying degrees depending on species, loose territoriality or site related dominance (Maher and Lott, 1995). The size of this territory varies from one species to another; for example, the average diameter of a spotted antbird territory is 200m whilst for ocellated antbirds it is 500m (Willis, 1974). The pair will forage

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### 5.1. ANT BIRD NATURAL HISTORY

at swarms of *Eciton burchelli* or *Labidus praedator* (another swarm raiding army ant) should one be present on their own territory. Failing that, the pair will search for swarms further afield in neighbouring territories, and should any be found, they may, though not necessarily, forage there. If no raids can be found, or found but rejected, the pair will forage on the forest floor away from any swarm. When foraging at a swarm in its own territory, the antbird occupies the centre of the fan (see appendix B, figure 1) — the optimal foraging position. Without exception, it dominates all other birds of its own species (Willis, 1967). As the colony moves, the raid may leave one bird's territory and enter another and immediately the order of dominance will change — the once dominant antbird will find itself competing at the fringes of the swarm. The further the swarm is from a bird's own territory, the lower down the "pecking order" the antbird will find itself (Willis, 1967). Eventually, once the colony moves too far away from the antbird's nest site, or fails to send out a raid, it is abandoned and a new swarming colony is sought. The antbirds require a regular supply of food and so favour reliable food sources; clearly those colonies in the nomadic phase where raids occur daily as opposed to the stately phase where raiding takes place nearly every other day (Willis, 1967, see also section 1.1). The antbirds also favour *Eciton burchelli* colonies over *Labidus praedator* as the latter has less predictable raids and often raids underground or at night. In comparison, *Eciton burchelli* raids above ground and only during daylight hours.

Of the 238 types of antbirds, eleven were found upon Barro Colorado Island at its formation (Willis, 1974). Over the subsequent eighty years, the number of professional ant-following birds (i.e. their main resource is the ant swarms) has declined on the island to the three or four species found today, while their food supplies, army ant colonies, have not changed in abundance. Certain species have declined in number to the point of extinction, while others remain as abundant as when BCI was first formed. For example, the ocellated antbird is now extinct on Barro Colorado Island but the spotted antbird population remains stable. At the same time, the mainland populations in the forest on the edge of Gatun Lake have the same number and variety

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### 5.1. ANT BIRD NATURAL HISTORY

as eighty years ago.

There is a very important issue here. As the rain forests are being cleared, the remaining habitat often consists of small isolated fragments, which as has already been stated, are essentially no different from islands surrounded by water. Thus we could expect the antbird populations in these remnants to undergo the same changes as on Barro Colorado Island, meaning global extinction for many species of antbirds, which in turn would imply global extinction of all those species reliant on antbirds, such as the antbutterflies (Ray and Andrews, 1980) who feed on antbird droppings. Thus it is important to understand why antbirds are disappearing on Barro Colorado Island because only then can a conservation program be formulated. The common suggestion usually involves predation (see, for example, Willis, 1974; Crooks and Soulé, 1999). Being a small island (approx. 1500 hectares) and having a human population, Barro Colorado Island has a lack of top level predators such as pumas, jaguars and other large carnivores (Willis, 1967; Rubinoﬀ and Leigh, 1990). Without this highest trophic level, which is of course present on the larger nearby mainland, the next trophic level down faces reduced competition and predation and so their numbers flourish. It is these animals, such as monkeys and snakes, which predate the antbirds and especially their nests (Willis, 1967). It is interesting to note, however, that no animal has ever been caught in the act of predating an antbird nest, but many disturbed nests bear the hallmarks of a snake attack. Whilst increased predation rates explains why the bicolored antbird is going extinct on BCI and not on the mainland, it fails to explain why the spotted antbird is not in decline. It too is facing a higher predation rate but the demographic data does not show a decrease in numbers (Willis, 1974). In the following section, the first test of this conjecture is made by means of a simple mathematical model.

## 5.2 Heuristic Model

For simplicity, we consider only two competing antbird species, one a superior competitor who dominates the other species at a swarm and the other a superior exploiter who

is better at foraging away from a swarm. (Thus the superior competitor could describe the bicolored antbird while the superior exploiter could describe the spotted antbird.) Since nearly all females are in breeding pairs and only breeding pairs contribute to population growth, we consider only females numbers.

For the superior competitor, we make the following assumptions:

- No adult dies from starvation, only predation and senescence (recall, antbirds can forage away from swarms)
- There exists a maximum number of young an antbird can raise in a year
- Nesting success is independent of the age of a bird
- When foraging in their own territory, an antbird faces no competition either at or away from an ant swarm
- At swarms in neighbouring territories, an antbird faces intra-specific competition only
- The best food source is from swarms in their own territories, then swarms in neighbouring territories and finally away from swarms
- Availability of food limits how many young can be reared.

For the superior exploiter we make similar assumptions, namely

- Adult death is caused by predation, senescence and starvation
- There exists a maximum number of young a pair can raise in a year
- Nesting success is independent of the age of a bird
- When foraging in their own territory an antbird faces competition from the superior competitor only
- When foraging at a neighbouring territory the bird faces both inter- and intra-specific competition

- When foraging away from swarms an antbird has no competition
- The best food source is from swarms in their own territory, then at swarms in a neighbour's territory followed by foraging away from ant swarms
- Availability of food items limits how many young can be reared.

Let  $N_t$  and  $M_t$  denote the number of adult females of the superior competitors and exploiters respectively in year  $t$ . The model requires further parameters, as outlined in table 5.1. The assumptions previously stated enforce certain conditions on the

Parameter	Description
$c_N$ ( $c_M$ )	Strength of intra-specific competition for $N$ ( $M$ )
$\alpha_N$ ( $\alpha_M$ )	Annual female adult mortality rate for $N$ ( $M$ )
$\beta_N$ ( $\beta_M$ )	Female juvenile mortality rate for $N$ ( $M$ )
$n_N$ ( $n_M$ )	Maximum number of successful broods raised by a single $N$ ( $M$ ) per year in absence of predation
$p_1^N$ ( $p_1^M$ )	Proportion of time $N$ ( $M$ ) spends following swarms in own territory
$p_2^N$ ( $p_2^M$ )	Proportion of time $N$ ( $M$ ) spends following swarms in neighbouring territory
$r_1^N$ ( $r_1^M$ )	Relative amount of food found at neighbour's swarm by $N$ ( $M$ ) compared to own swarm
$r_2^N$ ( $r_2^M$ )	Relative amount of food found away from swarms by $N$ ( $M$ ) compared to own swarm
$c$	Strength of competition of $N$ over $M$

Table 5.1: A description of the parameters used in the simple model

parameters of table 5.1. Since there exist three possible foraging alternatives (at an antbird's own swarm, at a neighbour's swarm or away from swarms),  $p_1 + p_2 \leq 1$  for both  $N$  and  $M$ . Furthermore, it was assumed that the best food source was at one's own swarm, then at a neighbour's swarm (should one exist) and finally away from swarms entirely. Hence  $1 > r_1 > r_2 > 0$  for both  $N$  and  $M$ . By its very nature, when foraging away from swarms the superior exploiter is able to use its resources better than the superior competitor, hence the inequality  $r_2^M > r_2^N$ .

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## 5.2. HEURISTIC MODEL

### 5.2.1 Single Bird Dynamics

First, consider the dynamics of the dominant competitor  $N$ , since it is assumed to be unaffected by the subordinate species  $M$ . The probability an adult survives the year is  $1 - \alpha_N$ , so at time  $t + 1$ , there will be  $(1 - \alpha_N)N_t$  adults who have survived from the previous year. Furthermore, if  $f(N; p_1^N, p_2^N)$  denotes the expected number of young females produced by each bird per year given the foraging strategies  $p_1^N$  and  $p_2^N$ , then in year  $t$  there will be  $f(N; p_1^N, p_2^N)N_t$  juvenile birds of which a proportion  $1 - \beta_N$  will survive to become adults. Hence the dynamics of  $N_t$  takes the form

$$N_{t+1} = [(1 - \alpha_N) + (1 - \beta_N)f(N; p_1^N, p_2^N)] N_t. \quad (5.1)$$

Consider now the simplest function  $f$  which satisfies the above assumptions. Recall, it is assumed there exists a maximum number of young that a bird can rear each year; hence  $f$  must be bounded above by  $n_N$ . It is also assumed that foraging at one's own swarm provides the best food supply, so for fixed  $p_2^N$ ,  $f(N; p_1^N, p_2^N)$  must be an increasing function of  $p_1^N$ . Similarly, for fixed  $p_1^N$ ,  $f$  must be an increasing function of  $p_2^N$ . Thus we demand

$$0 \leq f(N; 0, 0) < f(N; 0, 1) < f(N; 1, 0) \leq n_N.$$

Furthermore, it is necessary to include competition for a bird foraging at neighbouring swarms; we use the negative exponential function as a simple model. (This has no real or mechanistic meaning — it is simply a decreasing function in the range  $[0, 1]$ . Indeed, we show in appendix C that similar behaviour is obtained with a different choice of this function.) Thus we choose  $f$  to be

$$f(N; p_1^N, p_2^N) = n_N [p_1^N + r_1^N \exp\{-c_N N\} p_2^N + r_2^N (1 - p_1^N - p_2^N)].$$

Notice the term inside the square brackets is bounded above by 1 ensuring  $f < n_N$ . The  $p_1^N$  term within the brackets denotes food obtained at one's own swarm. For a

proportion  $p_2^N$  of the time, the antbird is foraging at a neighbouring swarm, where the relative value of its food will be  $r_1^N$  compared to having a swarm of its own. The exponential term models competition between birds foraging at neighbouring swarms. The third term, corresponding to foraging away from swarms, has no competition built in since the antbird forages away from other birds.

Substituting this function into (5.1) yields the difference equation describing the population dynamics of the superior competitor

$$\begin{aligned} N_{t+1} &= F(N_t) \\ &= \left\{ (1 - \alpha_N) \right. \\ &\quad \left. + (1 - \beta_N)n_N [p_1^N + r_1^N \exp\{-c_N N_t\} p_2^N + r_2^N(1 - p_1^N - p_2^N)] \right\} N_t. \end{aligned} \quad (5.2)$$

It is easily shown that the steady states of (5.2) are  $N^* = 0$  and

$$N^* = -\frac{1}{c_N} \ln \left\{ \left[ \frac{\alpha_N}{(1 - \beta_N)n_N} - p_1^N - r_2^N(1 - p_1^N - p_2^N) \right] \frac{1}{r_1^N p_2^N} \right\}. \quad (5.3)$$

The non-trivial steady state (5.3) makes sense biologically if and only if  $N^* > 0$ , i.e. precisely when

$$\left[ \frac{\alpha_N}{(1 - \beta_N)n_N} - p_1^N - r_2^N(1 - p_1^N - p_2^N) \right] \frac{1}{r_1^N p_2^N} \in (0, 1)$$

which, upon rearranging, yields the condition

$$\left[ \frac{\alpha_N}{(1 - \beta_N)n_N} - p_1^N - r_2^N(1 - p_1^N - p_2^N) \right] \in (0, r_1^N p_2^N). \quad (5.4)$$

We shall henceforth restrict our parameters to satisfy this condition.

### 5.2.2 Extension to Two Competing Species

The dynamics of the inferior competitor (or superior exploiter),  $M$ , will be similar to those of the superior competitor,  $N$ , and in fact identical in the absence of  $N$ . More-

over, it is assumed that since the superior competitor always out-competes the inferior competitor, the dynamics of  $N$  will be unchanged by  $M$ ; a reasonable assumption as long as food supplies are not scarce and recover quickly. There is an abundance of insect prey fleeing ant swarms and hence this assumption is reasonable.

Proceeding in a similar manner as in section 5.2.1, the equation describing the growth of  $M$  over time is assumed to take the form

$$\begin{aligned} M_{t+1} &= G(N_t, M_t) \\ &= \{f(N_t, M_t) + g(N_t, M_t)\} M_t \end{aligned} \quad (5.5)$$

where  $f(N, M)$  denotes the probability an adult female survives the year and  $g(N, M)$  denotes the expected number of juvenile females surviving to reproduce in the following year.

It is assumed that adult females die through senescence, predation and starvation. To this end, let  $f(N, M)$  be the simplest function which decreases with  $N$  but also is similar to the comparable term in the dynamics of the superior competitor. Thus we choose

$$f(N, M) = (1 - \alpha_M) \exp \{-cN\} \quad (5.6)$$

where  $\alpha_M$  is the annual death rate in the absence of competition and is  $c$  the strength of inter-specific competition between  $N$  and  $M$ . Notice that  $f$  satisfies  $0 \leq f(N, M) \leq 1$  as stipulated above.

In the same fashion as in section 5.2.1 for the single antbird case, let the function  $g$  be given by

$$g(N, M) = (1 - \beta_M) n_M \left[ p_1^M e^{-cN} + r_1^M e^{-cN} e^{-c_M M} p_2^M + r_2^M (1 - p_1^M - p_2^M) \right]. \quad (5.7)$$

Clearly, the non-negative term inside the square brackets is bounded above by 1 so that  $g$  is bounded above by  $n_M$  — the maximum number of young that can be reared



in a year. The first term in the square brackets derives from a bird foraging at its own swarm where it faces competition only from the superior competitor  $N$ . The middle term denotes feeding at a neighbouring swarm where competition comes from both  $N$  and  $M$ . The third term represents foraging on one's own territory, away from any swarm, and hence away from any competition. The  $(1 - \beta_M)$  factor represents the proportion of juvenile birds surviving the year to breed.

Substituting (5.6) and (5.7) into (5.5) yields the non-linear difference equation describing the population dynamics of  $M$ :

$$\begin{aligned} M_{t+1} &= G(N_t, M_t) \\ &= \left\{ (1 - \alpha_M) \exp(-cN_t) + (1 - \beta_M) n_M \left[ p_1^M \exp(-cN_t) \right. \right. \\ &\quad \left. \left. + r_1^M \exp(-cN_t) \exp(-c_M M_t) p_2^M + r_2^M (1 - p_1^M - p_2^M) \right] \right\} M_t. \end{aligned} \quad (5.8)$$

Notice that (5.8) has an identical form to (5.2) when  $N = 0$  since both populations describe antbirds with similar behavioural ecologies.

### 5.2.3 Stability Analysis

We now determine the steady states of the dynamical system described by (5.2) and (5.8). Since the dynamics of the superior competitor  $N$  is unaffected by  $M$ , its steady states  $N^*$  are calculated as before — see equation (5.3). The steady states of  $M$  can thus easily be shown to be  $M^* = 0$  and

$$M^* = -\frac{1}{c_M} \ln \left\{ \left[ \frac{1 - (1 - \alpha_M) e^{-cN^*}}{(1 - \beta_M) n_M} - p_1^M e^{-cN^*} - r_2^M (1 - p_1^M - p_2^M) \right] \frac{1}{r_1^M p_2^M e^{-cN^*}} \right\}. \quad (5.9)$$

This nontrivial equilibrium is biologically meaningful if, and only if,  $M^* \geq 0$  which is easily shown to be equivalent to the condition

$$\left[ \frac{1 - (1 - \alpha_M) e^{-cN^*}}{(1 - \beta_M) n_M} - p_1^M e^{-cN^*} - r_2^M (1 - p_1^M - p_2^M) \right] \in (0, r_1^M p_2^M e^{-cN^*}). \quad (5.10)$$

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There are thus four possible steady states in which the system described by (5.2) and (5.8) can lie, corresponding to coexistence,  $N$  only,  $M$  only or extinction. It is desirable to determine the stability of each of these equilibria. Ideally one needs to show the eigenvalues

$$\begin{aligned}\lambda_1 &= (1 - \alpha_N) + (1 - \beta_N)n_N [p_1^N + e^{-c_N N} r_1^N p_2^N + r_2^N (1 - p_1^N - p_2^N)] \\ &\quad - N(1 - \beta_N)n_N r_1^N p_2^N c_N e^{-c_N N} \\ \lambda_2 &= (1 - \alpha_M)e^{-c_N} + (1 - \beta_M)n_M \\ &\quad [p_1^M e^{-c_N} + e^{-c_M M} e^{-c_N} r_1^M p_2^M + r_2^M (1 - p_1^M - p_2^M)] \\ &\quad - M(1 - \beta_M)n_M e^{-c_N} r_1^M p_2^M c_M e^{-c_M M}\end{aligned}$$

belonging to the Jacobian of the linearised system of (5.2) & (5.8) evaluated at the steady states lie within the unit circle. Unfortunately, the algebra is such that this exercise is impossible, so we resort to phase plane analysis, noting that since this is a discrete time dynamical system, phase plane analysis can only suggest certain behaviours and not confirm them.

Differentiating (5.8) along the isocline yields

$$0 = c(1 - \alpha_M)e^{-c_N} + (1 - \beta_M)n_M \times \left[ c p_1^M e^{-c_N} + c_M \frac{dM}{dN} e^{-c_M M} e^{-c_N} r_1^M p_2^M + e^{-c_M} c e^{-c_N} r_1^M p_2^M \right]$$

and since it is known that every term except  $dM/dN$  is positive, we conclude that  $\frac{dM}{dN} < 0$  and so the isocline corresponding to  $M$  is a decreasing function of  $N$ . Typical phase planes are shown in figure 5-1.

When the parameters allow competitive coexistence, the phase portraits suggest this equilibrium should be stable. Numerical simulation of equations (5.2) and (5.8) further confirm this belief. The other equilibria, corresponding to single species persistence or extinction, are clearly unstable.

When only single species persistence is possible it appears through both phase plane analysis and numerical simulation that these nontrivial steady states are stable while

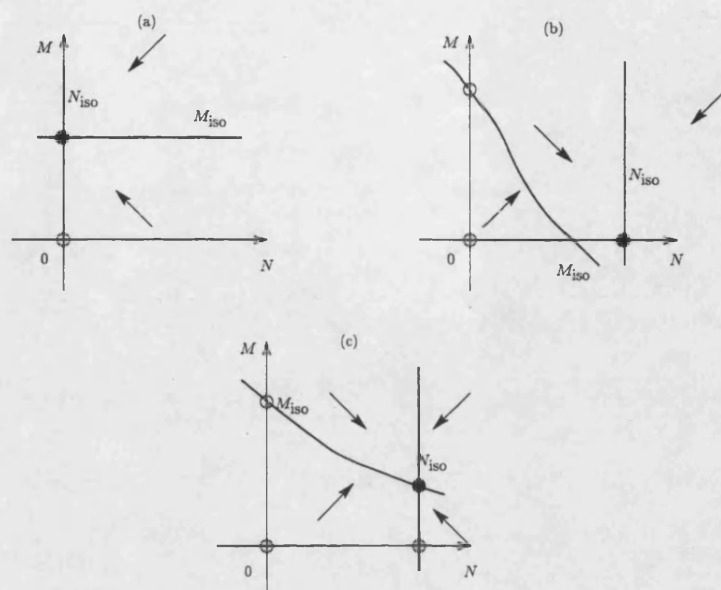


Figure 5-1: Typical phase portraits resulting from equations (5.2) and (5.8). Open circles denote unstable equilibria while solid circles denote possible stable steady states.  $N_{iso}$  and  $M_{iso}$  denote isoclines corresponding to  $N$  and  $M$  respectively. Since (a), (b) and (c) represent phase planes of a discrete time dynamical system, cyclic orbits cannot be ruled out, although numerical simulation suggests they do not arise.

extinction is unstable.

Finally when no species can exist, the only steady state,  $(0,0)$ , is clearly stable.

#### 5.2.4 Parameter Estimation

The model described above contains seventeen parameters which need to be evaluated. Fortunately, due to extensive fieldwork, especially by Edwin Willis (1967,1974), all but three of these parameters are known or can at least be approximated for three different antbirds, the bicolor antbird *Gymnopithys bicolor*, the spotted antbird *Hylophylax naeviodes* and the ocellated antbird *Phaenostictus mcleannani*.

The annual adult and juvenile mortality rates on Barro Colorado Island for the three antbird species highlighted above are given in Willis (1974). For convenience these values are repeated in table 5.2.

The  $r$ -values, which relate to comparable foraging abilities in different scenarios

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#### 5.2. HEURISTIC MODEL

<i>Bird</i>	<i>Annual adult mortality rate</i>	<i>Juvenile mortality rate</i>
Spotted antbird	0.16	0.6
Bicolored antbird	0.25	0.6
Ocellated antbird	0.30	0.4

Table 5.2: The annual mortality rate for three antbird species on Barro Colorado Island, Panama, as given in Willis (1974), for both adults and juveniles.

(i.e. at own swarm, at neighbouring swarm, away from swarms), may be obtained in the field simply by counting the number of prey items a bird consumes in a given day at each scenario. Unfortunately there is no data in the literature on this, but clearly the  $r$ -values must satisfy certain relationships:

- (i)  $1 > r_1^N > r_2^N$  and  $1 > r_1^M > r_2^M$  – the birds obtain more food at a swarm than away from it. They are called antbirds for a reason!
- (ii)  $r_2^M > r_2^N$  – the poorer competitor must survive somehow, and it does this by being a better forager away from swarms. Empirical evidence supports this (Willis, 1974).

The  $n$ -values, the maximum number of juvenile females that can be reared by a single bird in a year in the absence of predation, is found from dividing the length of the breeding season by the average time it takes to rear a single brood. For the spotted, bicolored and ocellated antbirds this value is 3 (Willis, 1974).

The parameters  $p_1$  and  $p_2$  are, surprisingly, not given in the literature, but they may be approximated via a computer simulation based on the behavioural description of antbirds given in Willis (1967) and Willis and Oniki (1978). Recall,  $p_1$  and  $p_2$  denote the proportion of time an antbird spends foraging at a swarm in its own territory and at a neighbouring territory respectively. (Here neighbouring does not necessarily refer to adjacent sites, but some region around the nesting territory.) Willis (1974) gives data on territory size for a variety of antbirds while Willis (1967) and Franks (1982b) calculate abundance of *Eciton burchelli* swarms on Barro Colorado Island, Panama (which is also representative of surrounding mainland forest). Using this data,

one can calculate the probability a given territory has an *Eciton burchelli* swarm. It transpires that colonies are randomly distributed throughout the rain forest and hence the spatial position of colonies is described by a Poisson distribution. However, because of the manner antbirds follow swarms on a day to day basis, one cannot necessarily approximate  $p_1$  and  $p_2$  from a Poisson distribution using data on territory size and army ant abundance. While colonies of *Eciton burchelli*, the preferred foraging choice, are random in space (Franks and Fletcher, 1983), the swarms are not necessarily random in time and space since the location of a colony on one day is closely related to its position on the previous day (either at the same site or about 91 metres away – the typical daily distance migrated during the nomadic phase (Franks and Fletcher, 1983)). Thus a Poisson approximation for  $p_1$  and  $p_2$  may not necessarily be ideal. To this end, a computer simulation was developed to convert antbird behaviour and territory size into information about  $p_1$  and  $p_2$ . The simulation was conducted on a square island of approximately 10 square kilometres with periodic boundary conditions applied to minimise edge effects. The number of *Eciton burchelli* colonies was assumed constant and set to be the density found on Barro Colorado Island, 3.5 colonies per square kilometre (Franks and Fletcher, 1983). The colonies then moved according to the well documented 35-day activity cycle consisting of a 20-day statary phase followed by a 15-day nomadic phase. Colonies were made to swarm according the reports of Willis (1967); every day during the nomadic phase, the first four and last four days of the statary phase and with probability  $1/2$  in the middle of the statary phase. For each species, antbird nests were established at the density given in Willis (1974) and the birds located and followed swarms according to the behavioural patterns in Willis (1967). Once a bird finds a swarming colony, it is followed until the ant colony fails to swarm or else moves too far away from the antbird's nest. This maximum distance depends on the species of antbird (see Willis, 1974, for data). When a colony is abandoned, either the closest swarm to the nest is followed (should one be within the maximum foraging distance) or else no *Eciton burchelli* swarm is followed and the antbird forages in its own territory, away from both competition and ant swarms.

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A simulation was run for a thousand days for each of the three antbirds considered in this section – the spotted antbird, the bicolored antbird and the ocellated antbird. Antbird birth and death was ignored, since the object of the simulation was irrelevant to these processes. The average time a bird spent foraging in the three scenarios was calculated and is presented in table 5.3.

<i>Foraging scenario</i>	<i>Proportion of time</i>		
	<i>Spotted</i>	<i>Bicolored</i>	<i>Ocellated</i>
Own swarm	0.12	0.16	0.49
Neighbouring swarm	0.54	0.68	0.39
Away from swarms	0.34	0.16	0.12

Table 5.3: The parameters  $p_1$  and  $p_2$  are calculated for the three different antbirds. Colonies are located, followed and abandoned as explained in the text. The simulation was conducted on an island of 10 square kilometres with periodic boundary conditions and antbird density typical of the antbird species (e.g. 6 territories per square kilometre for the bicolored antbird). The foraging position of each bird over 1000 consecutive days was noted and the mean proportion of time spent in each strategy was calculated to estimate  $p_1$  and  $p_2$ .

The final three parameters  $c$ ,  $c_N$ ,  $c_M$ , relating to the strength of competition between the species, are unknown. Although their meaning is clear, they are introduced in a very non-mechanistic sense, and it would be very difficult, if not impossible, to measure them in the field. For this reason, values of  $c$ ,  $c_N$ ,  $c_M$  are considered throughout their range  $(0, \infty)$ .

### 5.2.5 Results of Heuristic Modelling

For simplicity we assume that predation rates for both species of antbirds are the same; for bicolored and spotted antbirds this is a not unreasonable assumption (Willis, 1974). Figure 5-2 shows in  $\alpha$ - $\beta$  space, for a range of other parameters, how the steady state solutions (5.3) and (5.9) are influenced by predation rates. There appears to be a general pattern, typified in figure 5-3. The white regions correspond to competitive coexistence, the light grey corresponds to persistence of the subordinate competitor only, the dark grey to the dominant competitor only and the black region to extinction

of both types. Note in particular the higher predation hypothesis is supported by figure 5-3.

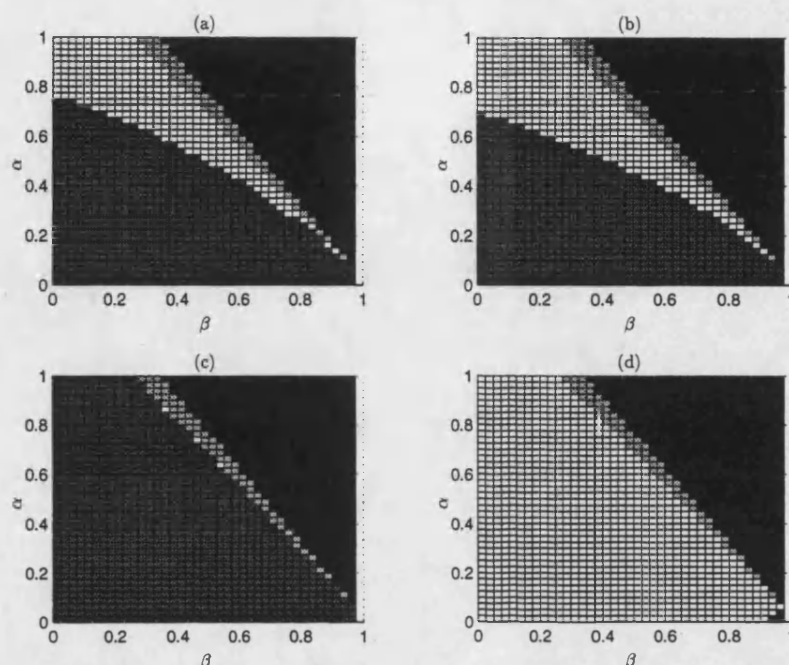


Figure 5-2: The four regions in  $\alpha - \beta$  parameter space correspond to the four different equilibria. The black region corresponds to the case when neither bird can persist, the dark grey to the superior competitor only, the light grey to  $M$  only and the white corresponds to competitive coexistence. The other parameter values are  $p_1^N = 0.16, p_2^N = 0.68, p_1^M = 0.12, p_2^M = 0.54, r_1^N = 0.4, r_2^N = 0.05, r_1^M = 0.5, r_2^M = 0.3, n_N = n_M = 3$ . In (a)  $c = c_N = c_M = 1$ , (b)  $c = 1, c_N = 1.5, c_M = 0.1$ , (c)  $c = 10, c_N = 0.1, c_M = 1.5$  and (d)  $c = 0.1, c_N = 10, c_M = 0.1$ .

### 5.2.6 Discussion of Heuristic Model

This simple model makes an important prediction regarding the order of extinctions among competing populations. In multi-species competition, the dominant competitor will be the worst disperser and likewise the worst competitor will be the best disperser, otherwise coexistence will be impossible (Tilman et al., 1994). The results of the simple model suggests the order of antbird extinctions on BCI should be from most dominant to least dominant. Table 5.4 shows the antbirds which were present on Barro Colorado

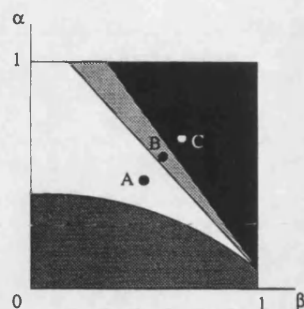


Figure 5-3: The four regions in  $\alpha$ - $\beta$  space correspond to the four different equilibria. The black region corresponds to the case when neither bird can persist, the dark grey to the superior competitor only, the light grey to  $M$  only and the white corresponds to competitive coexistence. Notice that slightly increasing the predation levels, corresponding to moving from point  $A$  to point  $B$ , causes the dominant competitor to go extinct. Increasing the predation rates still further, that is moving to point  $C$ , forces the inferior competitor extinct. Point  $A$  probably corresponds to parameter values found on the mainland around Gatun Lake where all the antbirds are present. Point  $B$  most likely corresponds to Barro Colorado Island, where the inferior competitor, i.e. the spotted antbird, persists as a stable population while the superior competitor, the bicolor antbird, is forced towards extinction. Possibly once the bicolor antbird is extinct on BCI, predation levels of the spotted antbird will rise still further, pushing BCI to point  $C$  and the spotted antbird population to extinction.

Island at its formation in decreasing order of dominance, and information on their date of extinction or current state is given. The field data appears to confirm the model's prediction.

The reason for this counter-intuitive order of extinctions is surprisingly straightforward. Under an increase in predation rates, abundances of both the superior and inferior antbirds initially decline. Since the dominant population is reduced, the inferior competitor faces less competition for resources and so obtains more food. This increase in food, which is then used to rear more young, will go towards offsetting the increased predation rates. Clearly this model cannot test this prediction, since as stated above quantitative questions cannot be answered by this model, but a mechanistic model, derived in section 5.3, can.

The model makes a further prediction which can be easily tested in the field. It was suggested above that the spotted antbird continues to persist on Barro Colorado Island by filling the niche created by the decline of the bicolor antbird. Thus a simple

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<i>Antbird</i>	<i>Approx. year of extinction</i>
Rufous-vented Ground-Cuckoo	Extinct prior to 1960
Barred Woodcreeper	Extinct by 1971
Ocellated Antbird	Extinct during 1970s
Plain-brown Woodcreeper	Unknown now, stable in 1960s
Bicolored Antbird	Currently close to extinction
Gray-headed Tanager	Still present, stable
Spotted Antbird	Still present, stable

Table 5.4: Data on antbird extinctions on Barro Colorado Island. The antbirds are listed in decreasing order of dominance. This table is compiled from references cited in this chapter, especially Willis (1974).

prediction of the model is that spotted antbirds on BCI spend more time foraging at *Eciton burchelli* swarms compared to spotted antbirds on the surrounding mainland since they face less competition on BCI than on the mainland.

This conclusion has a pleasant analogy with the work of Dave Tilman (Tilman, 1994; Tilman et al., 1994). He and his colleagues considered how competing species fare under habitat fragmentation. They assumed the best competitors were the worst dispersers and conversely the best dispersers were the worst competitors, much like it was assumed here that the best competitors were the poorest at foraging away from swarms. They concluded the best competitors were those who first went extinct through the effects of habitat fragmentation. Their result compares favourably with the above model where the best competitor was the first to go extinct under higher predation rates.

Despite the model being in good agreement with the data, there are numerous deficiencies in the model; in particular it is not mechanistic, especially in the manner competition is modelled via a negative exponential term. Indeed, the model's behaviour is not dependent on this term. In appendix C the simple model is reconstructed with the negative exponential terms being replaced by logistic terms. This revised model has the same equilibria and behaviour as the initial, and moreover stability analysis using the Jacobian of the linearised system is possible.

Furthermore, in single species dynamics the model fails to consider starvation as a

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cause of adult death — predation is the only means of dying. We commented above that the model, despite making good qualitative predictions, cannot be used for quantitative predictions for precisely these failings. For example, while the bicolored antbird is almost extinct from BCI, the spotted antbird density has been unchanged throughout the history of BCI. To overcome these problems, a second model, an energy-based mechanistic model, is derived in the following section.

### 5.3 A Mechanistic Model

The simple model of section 5.2 was seen to have numerous limitations, mostly arising because the model was not mechanistic. Because of this, important quantitative questions relating to the biology could not be answered, e.g. does increased predation alone explain why the bicolored antbirds are facing extinction while the spotted antbirds are a stable population? Here we derive an energy-based model (see also Schoener, 1976; Brown and Rothery, 1993), where terms such as inter- and intra-specific competition, fighting and travelling costs are explicitly included.

#### 5.3.1 Derivation of Mechanistic Model

Let  $N_t$  and  $M_t$  denote the number of adult females of the superior and inferior competitors in year  $t$  respectively. Further parameters are defined in table 5.5, such as total energy available at an *Eciton burchelli* swarm and energy spent fighting one another at army ant swarms. We assume scramble competition at swarms and do not differentiate between swarms in a bird's own territory or in a neighbouring territory, the differing energies should be averaged out over time making this a not unreasonable assumption. When foraging away from a swarm, it is assumed an antbird faces no competition.

Parameter	Description
$\alpha_N$ ( $\alpha_M$ )	Annual predation rate of $N$ ( $M$ )
$R_N$ ( $R_M$ )	Efficiency of $N$ ( $M$ ) in turning energy into young over one year
$I_S^N$ ( $I_S^M$ )	Energy at swarm in units for $N$ ( $M$ )
$\beta$	Probability $M$ gets food item compared to $N$ ( $\beta < 1$ )
$p_N$ ( $p_M$ )	Proportion of time $N$ ( $M$ ) spends foraging at army ant swarms
$I_A^N$ ( $I_A^M$ )	Energy foraged away from swarm by $N$ ( $M$ )
$\gamma_{NN}$ ( $\gamma_{NM}$ )	Energy spent per day by $N$ competing with a single $N$ ( $M$ )
$\gamma_{MN}$ ( $\gamma_{MM}$ )	Energy spent per day by $M$ competing with a single $N$ ( $M$ )
$E_T^N$ ( $E_T^M$ )	Energy spent by $N$ ( $M$ ) travelling unit distance
$d_N$ ( $d_M$ )	Typical foraging distances from swarm to nest for $N$ ( $M$ )
$C_N$ ( $C_M$ )	Energy required by $N$ ( $M$ ) to survive
$\lambda$	Density of <i>Eciton burchelli</i> swarms
$A$	Area of reserve

Table 5.5: The basic parameters used in the mechanistic model

Thus the dynamics for  $N$  and  $M$  can be described by

$$N_{t+1} = (1 - \alpha_N) \left\{ 1 + R_N \left[ \frac{I_S^N p_N}{p_N N_t + \beta p_M M_t} + (1 - p_N) I_A^N - \gamma_{NN} p_N \frac{p_N N_t}{\lambda A} - \gamma_{NM} p_N \frac{p_M M_t}{\lambda A} - p_N d_N E_T^N - C_N \right] \right\} N_t, \quad (5.11a)$$

$$M_{t+1} = (1 - \alpha_M) \left\{ 1 + R_M \left[ \frac{\beta I_S^M p_M}{p_N N_t + \beta p_M M_t} + (1 - p_M) I_A^M - \gamma_{MN} p_M \frac{p_N N_t}{\lambda A} - \gamma_{MM} p_M \frac{p_M M_t}{\lambda A} - p_M d_M E_T^M - C_M \right] \right\} M_t. \quad (5.11b)$$

The terms inside the square brackets denote the energy each bird can put into reproduction over a year. The first term,  $p I_S / (p_N N + \beta p_M M)$ , denotes the energy obtained from foraging at a swarm. The factor of  $p$  in the numerator simply allows for that resource to be obtained on any given day with probability  $p$ ,  $I_S$  denotes the overall energy available to a bird whilst  $(p_N N + \beta p_M M)$  denotes the number of birds (or more precisely the effective number of  $N$ ) foraging at swarms among which the energy  $I_S$  is evenly shared. Thus both  $N$  and  $M$  are competing for the same resource, dividing it such that each  $N$  gets a fraction  $1/(p_N N + \beta p_M M)$  of the overlapping resource and

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each  $M$  gets a fraction  $\beta/(p_N N + \beta p_M M)$ . This term implies an individual can utilise all of its resource share, an assumption which matters little near equilibrium but will give unrealistic dynamics when both  $N$  and  $M$  are small (see discussion in section 5.3.4). The second term,  $(1 - p)I_A$ , represents energy obtained whilst foraging away from swarms, each bird being able to obtain  $I_A$  units of energy for a proportion  $1 - p$  of the time; there is no competition for this resource. The next two terms involving  $\gamma$  denote energies spent fighting with other birds while foraging at an army ant swarm, the term  $pN/\lambda A$  simply describing the average number of superior competitors at a swarm. The term involving  $E_T$  accounts for energies spent flying from the nest to the swarm, a bird flying to a swarm for a fraction  $p$  of the year and covering a typical distance  $d$ . The final term  $C$  accounts for the basic survival costs for each bird over the course of a year. The remaining energy, if any, is channelled into reproduction, one unit energy being converted into  $R$  young females. As before, antbirds are predated at rate  $\alpha$ , so a proportion  $1 - \alpha$  of adults one year survive to breed in the following year.

### 5.3.2 Analysis of Mechanistic Model

Model (5.11) can yield a range of behaviours depending on certain parameter values. Here we consider what behaviours, especially what equilibria, are possible.

Evaluating (5.11a) at equilibrium  $(N^*, M^*)$  gives rise to the second degree equation for the  $N$ -isoclines

$$\begin{aligned} \frac{\gamma_{NN} p_N^3}{\lambda A} N^2 + \left( \frac{\gamma_{NM} p_N^2 p_M}{\lambda A} + \frac{\gamma_{NN} \beta p_N^2 p_M}{\lambda A} \right) NM + \frac{\beta \gamma_{NM} p_N p_M^2}{\lambda A} M^2 \\ + p_N \Phi_1 N + \Phi_1 \beta p_M M - I_S^N p_N = 0 \end{aligned} \quad (5.12)$$

where

$$\Phi_1 = \frac{\alpha_N}{(1 - \alpha_N) R_N} + C_N + p_N d_N E_T^N - (1 - p_N) I_A^N.$$

Equation (5.12) has a graph of a conic section whose type is determined by the dis-

criminant  $\delta_N$ ,

$$\begin{aligned}\delta_N &= (\gamma_{NM} + \beta\gamma_{NN})^2 \left( \frac{p_N^2 p_M}{\lambda A} \right)^2 - 4 \left( \frac{\gamma_{NN} p_N^3}{\lambda A} \right) \left( \frac{\beta\gamma_{NM} p_N p_M^2}{\lambda A} \right) \\ &= (\gamma_{NM} - \beta\gamma_{NN})^2 \left( \frac{p_N^2 p_M}{\lambda A} \right)^2.\end{aligned}\quad (5.13)$$

Clearly  $\delta_N$  is non-negative. When  $\delta_N = 0$ , the conic section given by (5.12) could be a pair of straight lines or a single point. However, for  $\delta_N > 0$ , the second degree equation (5.12) will describe a hyperbola.

Similarly, by examining (5.11b) at the steady state  $(N^*, M^*)$ , the second degree equation

$$\begin{aligned}\frac{\gamma_{MNP} N^2 p_M}{\lambda A} + \left( \frac{\beta\gamma_{MNP} N p_M^2}{\lambda A} + \frac{\gamma_{MMP} N p_M^2}{\lambda A} \right) NM + \frac{\beta\gamma_{MMP} p_M^3}{\lambda A} M^2 \\ + p_N \Phi_2 N + \beta p_M \Phi_2 M - \beta I_S^M p_M = 0\end{aligned}\quad (5.14)$$

is obtained for the  $M$ -isoclines where

$$\Phi_2 = \frac{\alpha_M}{(1 - \alpha_M)R_M} + C_M + p_M d_M E_T^M - (1 - p_M)I_A^M.$$

The discriminant of (5.14) is

$$\delta_M = (\beta\gamma_{MN} - \gamma_{MM})^2 \left( \frac{p_N p_M^2}{\lambda A} \right)^2, \quad (5.15)$$

and the equation (5.14) usually describes a hyperbola.

Hence the steady states corresponding to coexistence are given by the intersection of the two hyperbole (5.12) and (5.14). Further equilibria are, of course, found where the hyperbole intersect the  $N = 0$  and  $M = 0$  axes.

### Equilibria

The equilibria of the system (5.11) are given by the intersection of the zero-isoclines (5.12) and (5.14), and since these are usually hyperbola, there are usually at most four

internal steady states. In fact, as we now show, there can be at most two internal equilibria. Notice this analysis is independent of the discriminants (5.13) & (5.15).

Differentiating (5.11a) along the  $N$ -isocline with respect to  $M$  yields

$$0 = -\frac{I_S^N p_N}{(p_N N + \beta p_M M)^2} \left( p_N \frac{dN}{dM} + \beta p_M \right) - \frac{\gamma_{NN} p_N^2}{\lambda A} \frac{dN}{dM} - \frac{\gamma_{NM} p_N p_M}{\lambda A} \quad (5.16)$$

so that  $dN/dM|_{\hat{N}} < 0$  for the curve described by (5.12). Differentiating (5.16) with respect to  $M$  yields

$$0 = \frac{2I_S^N p_N}{(p_N N + \beta p_M M)^2} \left( p_N \frac{dN}{dM} + \beta p_M \right)^2 - \frac{I_S^N p_N}{(p_N N + \beta p_M M)^2} p_N \frac{d^2 N}{dM^2} - \frac{\gamma_{NN} p_N^2}{\lambda A} \frac{d^2 N}{dM^2}$$

so that along the curve described by (5.12),  $d^2 N/dM^2|_{\hat{N}} > 0$ . In exactly the same fashion, it can be shown that along the hyperbola given by (5.14),  $dN/dM|_{\hat{M}} < 0$  and  $d^2 N/dM^2|_{\hat{M}} > 0$ .

Thus we have two important properties:

- The zero-isoclines monotonically decrease
- The isoclines (if not linear) are concave.

These properties imply the existence of at most two equilibria in the positive quadrant. We thus have a variety of possible phase planes as outlined in figure 5-4. Note that time is discrete in this model, so this analysis acts purely as a rough guide to determine what dynamics are possible.

By examining the derivatives further, we can show that if the curves intersect, then they do so only once in the positive quadrant. Hence under certain conditions, (e) and (f) in figure 5-4 are impossible. Let  $N'|_{\hat{N}}$  denote the gradient of the isocline (5.12) and  $N'|_{\hat{M}}$  denote the gradient of the isocline (5.14). If either  $N'|_{\hat{N}} > N'|_{\hat{M}}$  or  $N'|_{\hat{N}} < N'|_{\hat{M}}$  for all values of  $(N, M)$  then, if the isoclines intersect, they do so only

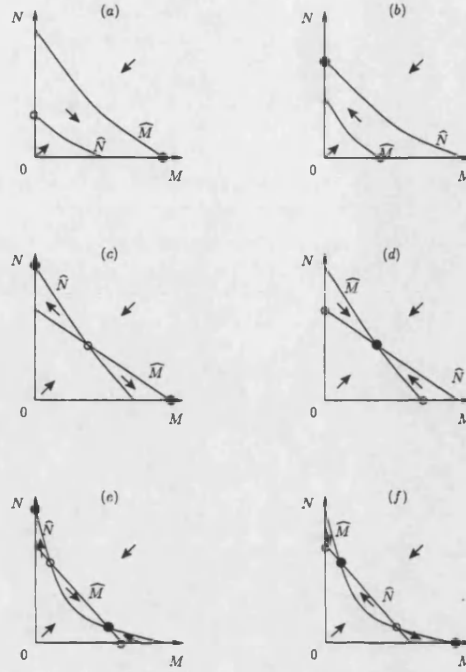


Figure 5-4: Some of the possible phase portraits given by model (5.11).  $\hat{N}$  and  $\hat{M}$  denote the zero-isoclines given by (5.12) and (5.14) respectively. Open circles denote unstable equilibria and shaded circles denote stable steady states. In all instances  $(0,0)$  is an unstable steady state. Note that time is discrete so limit cycles and chaotic population dynamics cannot be ruled out. In (a), (b) and (c) the only stable steady states are single species persistence. In (d), (e) and (f) there are stable coexistence equilibria.

once. To this end it is easily shown from (5.16) that

$$\begin{aligned} \frac{dN^*}{dM^*} \Big|_{\hat{N}} - \frac{dN^*}{dM^*} \Big|_{\hat{M}} = \text{const.} \times & \left\{ \lambda A I_S^N (\gamma_{MM} - \beta \gamma_{MN}) + \lambda A I_S^M \beta (\beta \gamma_{NN} - \gamma_{NM}) \right. \\ & \left. + (\gamma_{NN} \gamma_{MM} - \gamma_{NM} \gamma_{MN}) (p_N N + p_M \beta M)^2 \right\}. \end{aligned} \quad (5.17)$$

If the term in braces has constant sign for all values of  $N$  and  $M$ , then at most one intersection of the isoclines is possible. It is easily seen that two sufficient conditions

for a constant sign in (5.17) are

$$\gamma_{MM} > \beta\gamma_{MN} \quad \& \quad \beta\gamma_{NN} > \gamma_{NM} \quad \text{or} \quad (5.18a)$$

$$\gamma_{MM} < \beta\gamma_{MN} \quad \& \quad \beta\gamma_{NN} < \gamma_{NM}. \quad (5.18b)$$

When these conditions are satisfied the discriminants (5.13,5.15) are positive and hence the isoclines are hyperbole.

### 5.3.3 Results of Mechanistic Model

Here we investigate the effect of increased predation rates; as before focusing attention on the spotted and bicolored antbirds, which recall, have similar predation rates. Several of the other parameters are known, but most of those related to energy such as  $I$ ,  $E_T$  and  $C$  are not. These could in principle be obtained in the field, but here we are forced to rely on intuition to choose suitable values.

Figure 5-5, which is obtained from iteratively solving (5.11), shows that a sudden increase in predation rates forces the dominant antbird extinct while the inferior competitor continues to persist at similar demographic levels prior to increased predation.

### 5.3.4 Discussion of Mechanistic Model

The mechanistic model not only confirms the predictions of the earlier simple model concerning the order of antbird extinctions, but it is also in quantitative agreement with the data. It predicts that under increased predation the bicolored antbird will become extinct in about 80 years (in good agreement with the data) and also the spotted antbird population will remain stable at similar levels prior to the increased predation levels (again, in good agreement with the data). It is worth reiterating the reason for this, paying particular attention to the populations in figure 5-5. Under increased predation levels, initially both the superior and inferior antbird populations decline. However, once the dominant antbird population falls sufficiently low, the



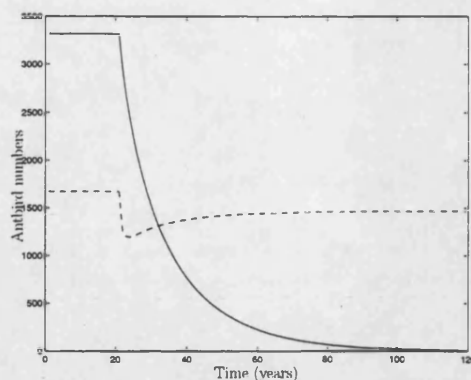


Figure 5-5: The equations (5.11) are started from their equilibrium with predation rates  $\alpha_N = \alpha_M = 0.2$  and solved iteratively for twenty time steps (i.e. twenty years). The equations then continue to be solved but with a higher predation rate,  $\alpha_N = \alpha_M = 0.3$ . This is supposed to mimic the formation of Barro Colorado Island, Panama, which was once a hill-top but now an island after the flooding of the surrounding lowlands. This isolation forced the top levels predators extinct, allowing their prey, antbird predators, to flourish. Other parameter values are chosen to reflect the environment on BCI  $\lambda = 2.7$ ,  $\gamma_{NN} = 10$ ,  $\gamma_{NM} = 9$ ,  $\gamma_{MN} = 9$ ,  $\gamma_{MM} = 20$ ,  $I_S^N = 1000$ ,  $I_S^M = 1000$ ,  $I_A^N = 100$ ,  $I_A^M = 500$ ,  $E_N = E_M = 10$ ,  $d_N = 0.5$ ,  $d_M = 0.3$ ,  $R_N = R_M = 1e - 06$ ,  $C_N = C_M = 2$ ,  $A = 15$  and  $\beta = 0.4$ . The  $p$  parameters are those calculated for the model of section 5.2. Various values for the energy parameters were examined with little qualitative effect on dynamics (not shown). Notice that conditions (5.18) are satisfied.

subordinate faces less competition at swarms, enabling it to obtain more energy from this source. This energy is turned into juvenile birds which allows the population to reach relatively similar levels as under the previous lower predation levels. Once again, a testable prediction of this model would be to compare the time spotted antbirds spend foraging at and away from swarms on BCI compared to the nearby mainland – the time spent at swarms on BCI should be more.

The energy based approach of the mechanistic model made quantitative predictions possible, but the manner in which the birds obtained most of their energy, via scramble competition, means the model has a major limitation. Recall, this aspect was modelled by a term of the form  $I/(N + \beta M)$ , where  $I$  denoted total available energy,  $N$  and  $M$  were the number of dominant and subordinate birds and  $\beta < 1$  was a measure describing the difference in dominance between the species. This term assumes all the available energy on the island can be exploited by all the antbirds – a very unrealistic

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### 5.3. A MECHANISTIC MODEL

assumption. For values of  $N + \beta M$  which are not too small, this assumption probably makes little difference (see also Schoener, 1976) but when  $N + \beta M$  is small, the model breaks down. To rectify this problem, the scramble competition term could be replaced by a term resembling

$$\max \left\{ \frac{I}{N + \beta M}, I_{\max} \right\}$$

where  $I_{\max}$  is an upper limit on how much energy a bird can obtain under no competition. The model will still have elements of scramble competition, but also maintain some realism with the birds having a foraging limit. Through this revised model, multi-species extinctions could be evaluated, a problem the previous design could not address.

The main goal of the modelling has now been achieved, i.e. to explain antbird extinctions on Barro Colorado Island. Naturally another interesting question now arises: What, if anything, can conservationists do to prevent the antbird extinctions? There are only two parameters which could possibly lend themselves to adaptation,  $I_A$  – energy found away from swarms and  $\alpha$  – adult predation rates. Artificially raising  $I_A$  by introducing antbird prey items has limited appeal – not only is this technique hard, but the implications of having higher densities of arthropods etc. are almost impossible to predict. A more desirable approach is to lower the predation levels by suitable management of antbird predators. These predators form the highest trophic level on the island, so that controlling their populations should assist in maintaining diversity on Barro Colorado Island. However, the situation for forest fragments not surrounded by water may be different. The top level predators, such as jaguars, are not present on BCI, but may be present in other remnants less used by humans, thus controlling the numbers of antbird predators there. This may imply that antbird predation rates are lower in such fragments than, for example, BCI, so the antbird extinctions on BCI may not be reflected within other forest remnants. Clearly this must be tested; if found to be true, then to preserve antbird numbers within forest fragments, conservationists would need to encourage the top level predators into such remnants.

## 5.4 Evolutionary Predictions for Antbirds

The loose territoriality of antbirds, as explained above, seems a strange phenomenon at first; it is not just confined to antbirds though, numerous other birds, certain mammals and lizards also display similar behaviour patterns (see Maher and Lott, 1995, and references within). Edwin Willis in his 1967 paper discussed how this form of territoriality may have evolved. To summarise his arguments, he conjectured the antbirds originally defended an exclusive territory neither leaving this territory or tolerating visitors. Over time, this rigid territory was relaxed, neighbours were tolerated, especially if neighbouring birds are related, and hence foraging distances from the nest increased. This meant the emigrating army ant swarms could be followed for longer periods of time, thereby increasing the food supply for the antbirds. Willis hence suggests that natural selection favours more tolerant and less territorial antbirds. This prediction, an almost impossible task to test empirically, can easily be examined by using the mechanistic model developed in section 5.3.

### 5.4.1 Description of Model

Consider a single antbird population on an island, termed the wild type. The birds obtain food by both scramble competition at swarms and by foraging on their own when there is no swarm nearby. Energy is spent travelling to swarms, fighting with other birds, reproduction and simply staying alive. Suppose a mutant bird is now introduced to this population which spends less energy fighting other birds (i.e. is more tolerant of its neighbours) and is prepared to travel further to reach swarms, while other behavioural aspects are identical to the wild type.

One further crucial assumption has to be made; the female offspring of each antbird pair is assumed to have the same characteristics as the mother. This assumption allows us to use the above mechanistic model and hence disregard the importance of sexual reproduction in antbird populations. Without this important assumption the model would need to account for random mating between birds having different genotypes. For such instances, the probability that a young antbird inherits a certain gene would

be related to the frequency of that gene in the population as a whole.

Thus we have the mechanistic model of section 5.3 where  $N(t)$  denotes the wild type population at time  $t$  and  $M(t)$  the mutant population:

$$N(t+1) = (1-\alpha) \left\{ 1 + R \left[ \frac{I_{SPN}}{p_N N(t) + p_M M(t)} + (1-p_N)I_A - \gamma_N p_N \frac{p_N N(t)}{\lambda A} - \gamma_N p_N \frac{p_M M(t)}{\lambda A} - p_N d_N E_T - C \right] \right\} N(t) \quad (5.19a)$$

$$M(t+1) = (1-\alpha) \left\{ 1 + R \left[ \frac{I_{SPM}}{p_N N(t) + p_M M(t)} + (1-p_M)I_A - \gamma_M p_M \frac{p_N N(t)}{\lambda A} - \gamma_M p_M \frac{p_M M(t)}{\lambda A} - p_M d_M E_T - C \right] \right\} M(t) \quad (5.19b)$$

where the parameters are those explained in table 5.5. Necessary conditions imposed on the parameters follow from the above assumptions, namely

- $\gamma_N > \gamma_M$  — the mutant is more tolerant of other birds
- $d_N < d_M$  — the mutant follow swarms further from their nest sites

### 5.4.2 Evolutionary Predictions

Equations (5.19) are solved iteratively on a computer using MATLAB starting from the  $N$ -only steady state with a single mutant antbird, shown in figure 5-6. Notice the mutant population forces the wild population extinct and thus the more tolerant, or less site-related dominant antbird is favoured by natural selection.

### 5.4.3 Discussion of Evolutionary Predictions

The mechanistic model (5.19), as illustrated in figure 5-6 appears to confirm Edwin Willis's 1967 prediction that natural selection favours more tolerant antbirds.

However, the model makes one weak assumption. It is assumed that putting less energy into fighting a bird obtains the same amount of resource, or said differently, it is assumed that there is little point in fighting. Clearly this is wrong — the birds are

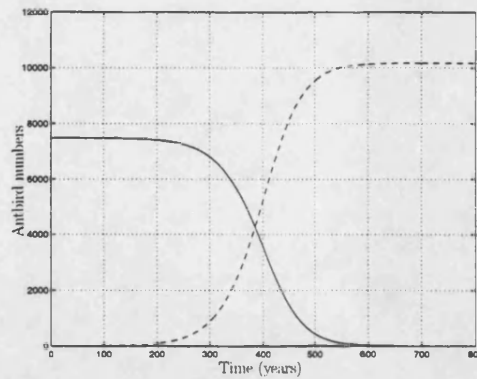


Figure 5-6: A more tolerant (mutant) antbird population (---) invades a less tolerant (wild) population (—) according to equations (5.19). The wild population is started from its equilibrium while the mutant population is initially a single individual. As time elapses, the mutants, spending less energy on fighting though more on travelling, increase in abundance and the wild population is gradually forced extinct. Since several of the parameter values are unknown, it is inadvisable to consider time scales as being relevant. The parameter values are  $\lambda = 2.7$ ,  $A = 15$ ,  $\alpha = 0.3$ ,  $\gamma_{NN} = \gamma_{NM} = 10$ ,  $\gamma_{MN} = \gamma_{MM} = 9$ ,  $I_S = 1000$ ,  $I_A = 100$ ,  $E = 10$ ,  $d_N = 0.5$ ,  $d_M = 0.51$  and swarms are assumed to be randomly distributed across the reserve.

competing for a common resource, should they not fight or compete for the resource, they receive none of it. In this sense, the scramble competition terms  $I/(N + M)$  and the interaction terms  $\gamma p \frac{pN}{\lambda A}$  are not independent. However, in fig. 5-6 the differences of energies spent in fighting by the rival birds was small, suggesting the advantages of fighting was small, but even so, less fighting and more tolerance were selected for; the model may not be as poor as one might first fear.

## 5.5 Summary

In this chapter the antbirds were introduced; a species of birds who closely associate with *Eciton burchelli* army ants in the tropical rain forests. Their natural history was summarised, with particular emphasis placed on the unusual, but not unique, loose territoriality system they adopt. It was noted that despite a constant food supply, certain antbirds have been, or are continuing to be, forced extinct on Barro Colorado Island, Panama, whilst others antbirds persist as stable populations. This has important con-

ervation implications since the antbirds are exceptionally poor dispersers and a forest fragment is in effect no different from an island surrounded by water. A commonly stated cause of such extinctions relates to the higher predation rates of antbirds on the island compared to surrounding mainland.

At first, a simple mathematical model was constructed to test the hypothesis. The initial model was purely heuristic and hence useful for only qualitative predictions, but it was seen that the hypothesis held: namely increased antbird predation rates could force certain antbirds extinct, and moreover forces them extinct in their order of dominance. This was seen to agree with the field data. The numerous limitations of this model were discussed and a mechanistic model was subsequently developed to account for these shortcomings. This new model was energy based, and hence gave quantitative predictions. It was seen that the hypothesis held and also agreed with the data on a quantitative scale regarding bird numbers. Finally the mechanistic model was used to test a conjecture offered by Edwin Willis to explain how antbird territoriality evolved. It was shown that birds defending exclusive territories fare worse than those who allow visitors and travel to neighbouring territories. Natural selection thus favours more tolerant and less site-related-dominant birds.

## Chapter 6

# Why Are Driver Ant Colonies So Large?

Typically when studying population dynamics, one obtains birth and death rates dependent upon the population density. In doing so, one assumes all members of a population are identical; for example, each gives rise to the same number of progeny. However, populations are collections of individuals, and an individual is precisely that. They may vary from one another in different ways, be it age, or size, etc. and these differences often account for variations in survival and reproductive rates; it is therefore necessary at times to include such differences (e.g Hassell and May, 1985). For example, in *Eciton burchelli* colony size is closely related to both colony birth and colony death.

There are also biological questions surrounding individual size; for example, why are animals (or plants) the size they are? The theory of natural selection answers this easily: it is because by being that size they fare better in a given environment than being any other size. More precisely, the population genetics are at an equilibrium, and should a mutation arise having slightly different size, it will be selected against. One often finds that different environments select for different characteristics, army ants provide an interesting case of this.

So far we have only considered the American army ant *Eciton burchelli*, yet there

are numerous other army ant species around the world (for example African Driver ants) which have evolved independently of one another. They exhibit many similarities with one another, but also stark differences (for example, colony size in Driver ants is much larger than *Eciton burchelli*). In this chapter we consider the African army ant *Dorylus molestus*, compare it to the American army ant *E. burchelli* and consider especially why the average colony size is so different between the two species.

In section 6.1 the natural history of the African army ant *Dorylus molestus* is introduced. Like *Eciton burchelli* it is a swarm raider, feeding on insects and arthropods and is pursued by ant following birds; yet there are numerous differences as is explained. The major difference between the two species is the average colony size, *Dorylus molestus* colonies being typically 40 times larger than *Eciton burchelli* colonies. A hypothesis to explain this size difference is then given, termed the fighting hypothesis. To test the hypothesis, two mathematical models are derived. The first, a size-structured Leslie matrix model, is the attention of section 6.2. In this section a model based on Leslie (1945) is established to describe how a structured population changes over time. The population has several parameters associated with it, for example, the size and manner of colony reproduction and the likelihood of fighting rival colonies upon colony collision. The optimum reproductive strategy is then obtained by comparing how each strategy compares against all other strategies. This process is repeated for two different environments, one mimicking the African environment and the other the Central American environment. After much computation, which may be minimised by establishing a useful property, the model is seen to favour larger colonies in the African environment and smaller colonies in the Central American environment, thus supporting the fighting hypothesis. Furthermore, the reproductive strategies favoured by the models are precisely those found in the field. In section 6.3 a second model using partial differential equations is developed, colony size now being measured continuously. Examining this model at the equilibrium gives bounds for the population distribution, which in turn yield information on maximum colony size and colony density. The model's predictions are seen to be in excellent quantitative agreement with the field data, and provide

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further evidence supporting the fighting hypothesis.

## 6.1 Driver Ant Natural History

Until now, this thesis has only considered the South and Central American army ant *Eciton burchelli*, and yet, as mentioned in chapter 1, there are numerous other army ant species distributed around the globe. Outside of the Americas, probably the most studied species are the Driver ants of Africa, but even so, there is little quantitative data on this or any other army ant species. Like *E. burchelli*, *Dorylus molestus* is a swarm raider, often followed by birds, and such are their similarities it is easier to highlight their differences.

### Colony and Worker Size

The most striking difference between the old and new world species is their size; *Dorylus molestus* colonies can contain up to twenty million worker ants, forty times the size of the largest *Eciton burchelli* colony (Hölldobler and Wilson, 1990). An obvious question arises: Why are *Dorylus molestus* colonies so much larger than their new world counterparts? Before offering an answer to this question, it is desirable to continue to state the other differences between the two species. Whilst the mean colony size is larger in the African species, mean worker size is much smaller; this places a larger emphasis on group retrieval of prey items within old world colonies (Franks et al., 1999).

### Colony Reproduction

Colony reproduction occurs through a process of colony division in both ant species, yet the precise nature of the division differs greatly. Whilst *E. burchelli* colonies split evenly in half once reaching sufficient size, typically taking three years to do so, *Dorylus molestus* colonies simply throw off small groups at short intervals (Leroux, 1979), much like afterswarms in honey bees (Seeley, 1985). There are also differences in timing; *Eciton burchelli* colonies will split only during the dry season whereas *Dorylus molestus* division occurs all year round.

### Lifestyle

*Eciton burchelli* has a well documented 35-day activity cycle consisting of a 20-day statary phase followed by a 15-day nomadic phase, but in *Dorylus molestus* there is no such regular cycle, although colonies alternate between statary and nomadic phases (Gotwald and van Someren, 1990; Gotwald, 1995). It appears that when food supplies run low, a *Dorylus molestus* colony simply ups and leaves for a new nest site, travelling for typically two to three days, before settling into a statary lifestyle lasting anywhere between 3 and 45 days (on average 14 days). Thus much more emigration occurs in the new world species, who spend approximately 40% of their lifetime travelling, than in the old world species, who in comparison spend about 14% of their lives moving home.

### Inter-Specific Competition

The prey items favoured by the new and old world species are different, *E. burchelli* preferring slower recovering social insects while *Dorylus molestus* prefers larger arthropods having faster recovery rates. This perhaps in part explains the lack of a regular activity cycle in the old world species. While *E. burchelli* colonies face much competition for their resource, they are on a high trophic level, *Dorylus molestus* colonies, on the other hand, are on a lower trophic level but face little inter-specific competition. Despite this lack of competition, *Dorylus molestus* colonies will fight for its resource, *Eciton burchelli*, on the other hand, have never been observed to fight one another.

### Intra-Specific Competition

A final important difference between the species is their relative abundance. *Dorylus molestus* colonies are on average three times as dense as *Eciton burchelli* colonies in their respective environments (Hölldobler and Wilson, 1990). Since colony density in the old world is much higher, it is natural that colonies collide frequently, and often when doing so they fight (Leroux, 1979); indeed, Gotwald (1995) observed four such fights over a 450 day period for a single colony. *E. burchelli* colonies on the other hand have mechanisms for avoiding each other (see, for example, Franks and Fletcher, 1983),

and on the few occasions colony collisions have been observed, no fighting occurred.

### 6.1.1 An Arms Race

An interesting question was raised above, namely, why are *Dorylus molestus* colonies so much larger than *Eciton burchelli* colonies? An answer to this question must involve at least some of the differences between the two species highlighted above. Notice that *D. molestus* colonies remain as large as possible throughout their lives whereas *E. burchelli* are very happy to become half as large as they once were (colony budding compared to colony fission). This difference suggests being small is truly a disadvantage in the African environment. Certainly, a problem with being small arises when two colonies collide and fight; the smaller colony should always be beaten by the larger. Hence, should colonies fight, it is an advantage for a colony to be as large as possible, suggesting an arms race within *Dorylus molestus*. Notice in *E. burchelli* colonies do not fight one another, maybe because the risk of losing some workers far outweighs the advantages gained by winning the fight. Hence being large in this species offers little advantage. A testable hypothesis is then "Fighting selects for larger colony size". We test this hypothesis by using two different mathematical models in the following sections.

## 6.2 Leslie Matrix Model

The simplest manner of modelling individual size explicitly is via a Leslie matrix model (see, for example, Leslie, 1945; Diekmann et al., 1986; Stearns, 1992). In such models the population is divided into discrete size classes and individuals grow or decay into other size classes according to certain rules related to their biology; thus a matrix can be formed describing individual size changes. Time can be either discrete resulting in a system of difference equations (e.g. Leslie, 1945; Stearns, 1992) or continuous yielding a set of ordinary differential equations (e.g. van den Bosch and Gabriel, 1997; Takada and Nakajima, 1998). Since both *Dorylus molestus* and *Eciton burchelli* colonies live by a discrete activity cycle, time is chosen to be discrete, one time step representing the average length of the activity cycle.

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### 6.2. LESLIE MATRIX MODEL

In the remainder of this chapter, when we refer to an individual's strategy, we mean the size at which it divides, the ratio of the split and how likely it is to fight other colonies. Two strategies can be compared by defining one of them to be the wild type and setting its population at equilibrium and introducing a single mutant using a different strategy and then examine whether the mutant can invade the wild type. We are thus seeking an Evolutionary Stable Strategy (ESS). The optimum strategy (or strategies) is defined here to be those which can invade all other strategies and are never forced extinct by any other strategy. (Thus the optimum strategy is computed in a similar fashion to the classic study of Axelrod and Hamilton 1981.)

Throughout this section we shall disregard the importance of random mating in a sexual population. That is we shall assume a daughter colony always displays the same characteristics (or strategy) as the parent colony. Without this important assumption the model would have to account for random mating by examining how a mutant genotype fared when introduced to a population consisting solely of a wild genotype. In the random mating model it would be assumed that the probability a daughter colony had a certain genotype (and hence displayed a certain reproductive strategy) would be related to the frequency of that genotype in the population as a whole.

### 6.2.1 The Model

To be consistent with the models of chapter 2, assume the habitat consists of an array of patches which are either young or old depending on the time since they were last occupied; let  $r$  denote the patch recovery time. Consider two rival strategies competing against one another; let  $N_i(t)$  denote the proportion of patches occupied by wild type colonies of size  $i$  at time  $t$ , and  $M_j(t)$  the proportion of patches occupied by size  $j$  colonies belonging to the rival strategy. Let  $n$  and  $m$  denote the number of size classes in the  $N$  and  $M$  strategies respectively and define

$$\hat{N} = \sum_{i=1}^n N_i, \quad \hat{M} = \sum_{i=1}^m M_i$$

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## 6.2. LESLIE MATRIX MODEL

as the total proportion of patches occupied by colonies of each strategy. As time progresses, the structure of each population changes according to

$$\begin{aligned} N_i(t+1) &= \sum_{j=1}^n P_{ij}(\mathbf{N}(t), \mathbf{M}(t)) N_j(t) \quad i = 1, \dots, n \\ M_i(t+1) &= \sum_{j=1}^m Q_{ij}(\mathbf{N}(t), \mathbf{M}(t)) M_j(t) \quad i = 1, \dots, m \end{aligned} \quad (6.1)$$

and so we may write  $\mathbf{N}(t+1) = P(\mathbf{N}(t), \mathbf{M}(t))\mathbf{N}(t)$ ,  $\mathbf{M}(t+1) = Q(\mathbf{N}(t), \mathbf{M}(t))\mathbf{M}(t)$  for suitable matrices  $P$  and  $Q$ . The matrices  $P$  and  $Q$  are easily defined once transition rules are specified explaining how colonies change size. To this end, assume

- If a colony gets in a fight, it fights according to Lanchester's square law and loses a certain amount of its workers (see later and also Franks and Partridge, 1993).
- If a colony does not fight and lands on a young patch, it decreases one population unit in size
- If a colony does not fight and lands on an old patch, it grows one population unit in size
- Colonies decaying to size 0 die
- Colonies growing beyond size  $n$  (or  $m$ ) divide somehow into smaller colonies.

The probability a colony fights during a time step is simply the probability it meets another colony multiplied by the probability it choose to fight this colony. Thus, if  $\gamma_N$  ( $\gamma_M$ ) denotes the probability an  $N$ -type ( $M$ -type) colony fights on encountering another colony, the probability an  $N$ -type ( $M$ -type) colony gets into a fight during a given time step is  $\gamma_N \times (\hat{N} + \hat{M})$  ( $\gamma_M \times (\hat{N} + \hat{M})$ ). We assume the outcome of colony fights is described by Lanchester's square law.

### Lanchester's Square Law

Consider two rival armies, one initially of size  $x_0$  and the other of size  $y_0$ , and let  $x(t)$  and  $y(t)$  denote the size of the respective armies at time  $t$ . Assume each army loses

soldiers at a rate proportional to the number of soldiers in the opposing army, thus

$$\frac{dx}{dt} = -\alpha y \quad \frac{dy}{dt} = -\alpha x \quad (6.2)$$

where  $\alpha$  is a constant of proportionality. Without loss of generality, assume  $x_0 > y_0$ . It is clear that the  $x$  army wins the battle and the  $y$  army loses. By solving (6.2) for  $y$  in terms of  $x$  and setting  $y = 0$ , the final number of  $x$ -type may be found to be  $\sqrt{x_0^2 - y_0^2}$ .

If a colony avoids fighting during a time step, in the mean field the probability it lands on an old patch is, as we have seen in chapters 2 & 3,  $(1 - \hat{N} - \hat{M})^r$  while one minus this number gives the chance of landing on a young patch if the colony does not fight. Ant colonies are governed by the rules of central place foraging since the more food the colony requires the further it has to raid from the nest spending progressively more energy in the process (see, for example, Sudd and Franks, 1987). For this reason, we introduce  $D$ , an upper limit on colony size, and assume colonies cannot grow beyond this size; the precise value of  $D$  will be determined solely by the environment. Finally, if an  $N$ -type colony grows beyond  $n$ , it divides into a number of smaller colonies of sizes  $p_1^n n, p_2^n n, \dots, p_k^n n$  where  $\sum p_i^n = 1$ . For notational purposes, we write this splitting strategy as  $[p_1^n n, p_2^n n, \dots, p_k^n n]$ . Similar dynamics are assumed for  $M$ -type colonies.

The optimum strategy is determined for two different environments, one describing Central America and the other Africa. In the American environment, prey recovery is slow and  $D$  is small; in Africa however, prey recovery is much faster and  $D$  is higher. The optimum strategy is obtained by repeatedly simulating equation (6.1) for different strategies using the computer package MATLAB. This computer intensive task may be lessened by use of property 6.1 established below.

Let  $N_t$  and  $M_t$  denote the size-structured populations of two rival phenotypes at time  $t$  which grow according to

$$\begin{aligned} N_{t+1} &= P(N_t, M_t)N_t \\ M_{t+1} &= Q(N_t, M_t)M_t \end{aligned}$$

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and suppose the exclusion steady states are given by  $\mathbf{N}^*$  and  $\mathbf{M}^*$ , i.e.  $\mathbf{N}^* = P(\mathbf{N}^*, \mathbf{0})\mathbf{N}^*$  and  $\mathbf{M}^* = Q(\mathbf{0}, \mathbf{M}^*)\mathbf{M}^*$ . Define the norm of a matrix  $R$  to be

$$\|R\| := \max\{|\lambda| : \lambda \text{ is an eigenvalue of } R\}.$$

We then have the following useful property:

**Property 6.1** *Suppose both strategies have exclusion stable steady states and define  $\lambda_P = \|P(\mathbf{0}, \mathbf{M}^*)\|$  and  $\lambda_Q = \|Q(\mathbf{N}^*, \mathbf{0})\|$ . where  $P$  and  $Q$  have the form specified above. Then if*

- (i)  $\lambda_P > 1$  and  $\lambda_Q > 1$ , either phenotype can invade the other and coexistence occurs
- (ii)  $\lambda_P > 1$  and  $\lambda_Q < 1$ ,  $\mathbf{N}$  can invade a population of  $\mathbf{M}$ 's, sending them extinct
- (iii)  $\lambda_P < 1$  and  $\lambda_Q > 1$ ,  $\mathbf{M}$  can invade a population of  $\mathbf{N}$ 's, sending them extinct.

### Results with Square Law Fighting

Recall from Lanchester's square law that when two armies having sizes  $x_0$  and  $y_0$  collide and fight, the smaller army dies while the larger army suffers casualties resulting in its population falling to  $\sqrt{x_0^2 - y_0^2}$  (assuming w.l.o.g.  $x_0 > y_0$ ). Thus, for example, a colony of size 5 will become a colony of size 3 only by fighting colony of size 4. Hence, if  $N_i$  denotes the proportion of patches occupied by colonies of size  $i$  and if  $\gamma$  denotes the probability of fighting upon colony collision, the transition probability for a colony to decay from size 5 to size 3 is given by  $\gamma N_4$ .

The optimal strategy was obtained for numerous environmental conditions, not just those reflecting America and Africa. Without exception, the optimal strategy always had split size  $D$ , the upper limit on colony size. In fact, any strategy which involved colony division at size  $D$  always invaded strategies which split at sizes less than  $D$ , although not necessarily forcing them extinct.

For fixed  $\gamma_N = \gamma_M \neq 0$ , i.e. we do not allow this aspect of the colony's behaviour to vary, the optimal split strategy is always, in the notation defined above,  $[D - 1, 1]$ ,

regardless of the environment, see for example figure 6-1(a). This highly non-symmetric splitting is consistent with observations made by Leroux (1979) for *Dorylus molestus*.

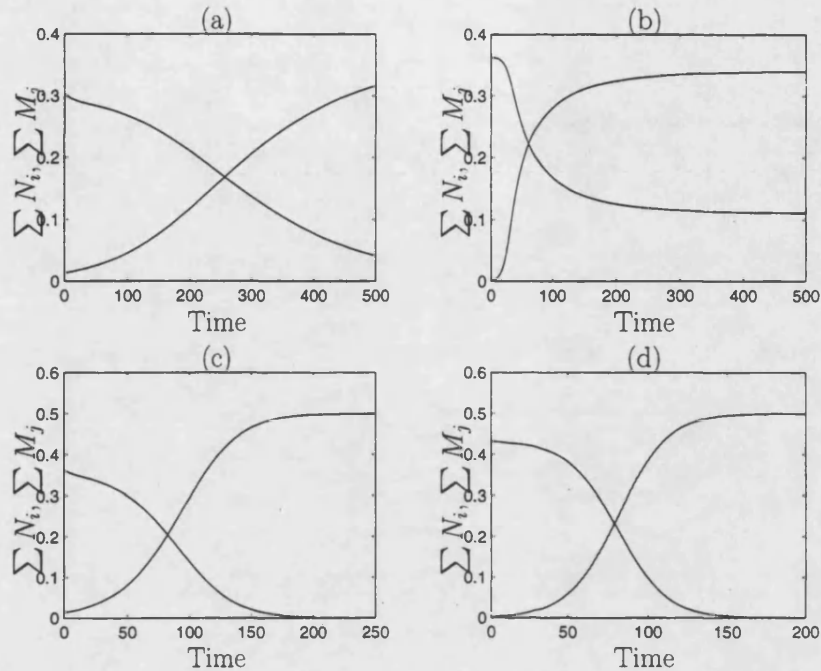


Figure 6-1: The equations (6.1) are solved iteratively on the computer for different strategies in two different environments; (a), (b) and (c) denote the African environment, (d) the American environment. (a)  $D = 15, r = 1$ : a  $[14, 1]$  strategy with  $\gamma = 0.2$  invades the more even splitting  $[7, 8]$  with  $\gamma = 0.2$ . (b)  $D = 15, r = 1$ : an early splitting  $[1, 1]$  strategy with  $\gamma = 0.2$  invades and coexists with the strategy  $[14, 1]$  with  $\gamma = 0.2$ . (c)  $D = 15, r = 1$ : the peaceful  $[14, 1]$  strategy with  $\gamma = 0$  invades and forces extinct the aggressive strategy  $[14, 1]$  with  $\gamma = 0.2$ . (d)  $D = 5, r = 6$ : the peaceful  $[2, 2]$  strategy with  $\gamma = 0$  invades and forces extinct the aggressive strategy  $[2, 2]$  with  $\gamma = 0.5$ .

If we define *selection strength* to be the rate which a mutant invades (or not, as the case may be) a wild population, the selection strength is higher for larger  $\gamma_N = \gamma_M$ . (That is with  $\gamma = 0.5$ ,  $[D - 1, 1]$  invades  $[D - 2, 1]$  much faster than  $[D - 1, 1]$  invades  $[D - 2, 1]$  with  $\gamma = 0.1$ .) Furthermore, selection strength is influenced by habitat recovery; the more rapid the habitat recovery, the greater the selection strength.

An interesting result concerns the coexistence of certain strategies which always arose when the mutant strategy  $N$  could invaded the wild  $M$ , and also the mutant strategy  $M$  could invaded the wild strategy  $N$ . When, say, the  $N$ -population is at the

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optimal strategy  $[D - 1, 1]$  for non-zero  $\gamma$ , other strategies can invade but not forcing  $N$  extinct, see figure 6-1(b). These strategies are of the form  $[1, 1]$ ,  $[2, 1]$ ,  $[2, 2]$ ,  $\dots$ ; the precise strategies depending upon  $D$ . While these opportunists nearly always loose fights, they have a sufficiently fast generation time to often avoid fighting. A bimodal distribution of predators, suggestive of competitive phenotype coexistence, has been recorded in species outside of ants (see examples in Dawkins, 1989; Rispe et al., 1998; Widemo, 1998).

We have failed so far to discuss the optimal strategy as a function of  $\gamma$ , a measure of the aggressiveness. Phenotypes with less ambition to fight, i.e. smaller  $\gamma$ , are always selected in favour of more aggressive phenotypes (Fig. 6-1(c) & (d)), making the overall optimal strategy  $[D - 1, 1]$  with  $\gamma = 0$ . This modelling hence suggests that *Dorylus molestus* colonies ought not to fight; yet they do! There is one possible explanation for this inconsistency. In the model, a colony gained little by fighting – it merely reduced competition by reducing the number of rivals. At the same time however, fighting reduced a colony's own fitness by the loss of soldiers during the battle. Hence the reason the model favoured non-fighting colonies simply reflected that the model did not give sufficient gains for winning a battle, gains which must exist in the field. For this reason, the model is adapted in the following section.

### 6.2.2 Non-Square Law Fighting

Previously it was assumed that colonies fought to the death and the only advantage gained by the victor was a reduction in competition for a common resource. It was seen that if the resource is abundant, as in the case for *Dorylus molestus*, fighting is never favoured by natural selection. Leroux (1979) and Gotwald (1995) reported that battles between two colonies rarely ended with the death of the loser, but usually one colony admitted defeat and retreated from the habitat patch. Often, but not always, the losing colony ended up of such small size it could no longer support itself and died soon after. The winning colony meanwhile, would not only conquer the habitat patch, but also feed on the dead soldiers, thus gaining considerably from victory. To this end

we adapt the fighting rules of the previous models.

### The Model

Every aspect of this revised model is identical to the previous except the outcome of battles. Here it is assumed the larger colony always wins the fight and the smaller loses; the winning colony gains the habitat patch and dead workers, and so grows one unit in size regardless of habitat quality, while the losing colony decreases one unit in size. When two colonies of the same size fight, both are assumed to decrease one unit in size; in effect both lose.

Two environments were considered, one reflecting the Central American environments faced by *Eciton burchelli* and the other resembling the African environment of *Dorylus molestus*.

### Results

As before, each strategy was started at its equilibrium state and in succession every other strategy was introduced and examined whether or not it invaded the wild type; this examination being conducted by repeated construction and multiplication of suitable matrices, and also by comparing how this fared with the predictions of property 6.1. Eventually, optimum strategies arose; i.e. those that could invade every strategy and were never forced extinct.

### Central American Environment

To mimic the environment faced by *Eciton burchelli* colonies in Central America, the parameter  $D$  was set to 4, while the time of patch recovery,  $r$ , was set to be 6. The optimal strategy, i.e. that which invaded every strategy and was never forced extinct by any other strategy was a colony with fight probability  $\gamma = 0$  adopting a  $[1, 1]$  split. Interestingly, the strategy  $\gamma = 0$  with a  $[3, 1]$  split, which recall was the optimum strategy under square law fighting, could not persist in this environment.

### African Environment

To reflect the environment of *Dorylus molestus* colonies in Africa,  $D$ , the density-dependent level, was set to be 15 and  $r$ , the patch recovery time, was set to be 1. In this instance the optimum strategy was for a colony to have a fight probability  $\gamma = 1$  and adopt a  $[14, 1]$  split. Again, as under square law fighting, early splitting strategies such as  $[1, 1]$  could coexist with the optimum strategy. However, the square law optimum strategy  $\gamma = 0$  with a  $[14, 1]$  split fared badly.

### Miscellaneous General Observations

Besides the results stated above, two other relationships arose:

**Patch recovery** Under all values of  $D$ , without exception, faster patch recovery always gave rise to higher population densities. This is agreeable with data on *D. molestus* and *E. burchelli* where the patch recovery time for the former is much more rapid than the later.

**Colony size** Whatever the environmental conditions, small colonies, i.e. early splitting strategies, never fared well if their fight probabilities were too high. Small colonies should avoid fighting as they have much less in reserve than larger colonies.

### Discussion of the Revised Model

The most pleasing aspect of this revised fighting model was its apparent agreement with the field data, i.e. the South American environment favoured smaller non-fighting colonies who split evenly while the African environment selected for larger fighting colonies whose reproductive strategy is to simply bud off small daughter colonies. This model's results are more consistent with the field data than the original square-law fighting, simply because there is a major advantage in winning a fight.

More importantly, the large differences between the two models suggests the outcome of fights is very important to the population dynamics as suggested by the fighting hypothesis. Since there is no quantitative data available, modelling this aspect is dif-

ficult. However, through the two fighting alternatives examined above, it is suggested the outcome of fighting lies somewhere between the square law and the outcome of the revised model. This prediction is easily testable by observing the outcome of fights between colonies.

### 6.2.3 Discussion of Leslie Matrix Models

The great advantage offered by Leslie matrix-based models is their simplicity; one needs only to describe the state transition laws and construct a corresponding matrix, repeated multiplication of this matrix gives the population changes. In this case, despite the model's simple construction, it predicts behavioural characteristics which have been observed in the field, i.e. colony size and fighting preference. In this sense, the model is a good one.

Although the model is simple, calculation of the optimum strategy is not a straightforward task; one needs to first find the steady state of the wild population, then introduce a single mutant type before examining the long term dynamics. This examination used repeated construction and multiplication of the transition matrices and was compared with property 6.1 – in all cases property 6.1 agreed with the more direct approach. Clearly, since there is a large number of strategies to compare, calculation of the optimum takes an enormous amount of computational time, be it for construction and multiplication of matrices, or calculation of eigenvalues.

Both the original and revised model contained few parameters, all bar one of which was known or may be found easily in the field; however,  $D$ , the level of density-dependence, is unknown and may not be a natural phenomenon. Density dependence must be included in the model to reflect issues such as those contained in central place foraging (Sudd and Franks, 1987), and without this restriction, progressively larger colonies always invade slightly smaller colonies resulting in the optimum colony size being infinite!

The main issue raised by the Leslie matrix modelling is that the fighting rules adopted by carnivorous ant species are not obvious. Whilst Franks and Partridge (1993)

and Partridge (1993) suggested army ants fought according to Lanchester's square law when combating prey species, there must be considerable advantage in winning a fight to offset the loss of many workers. This created a major problem in the modelling since there is a lack of any quantitative data on *Dorylus molestus* fights. It is commonly known, however, that the winning colony eats the dead soldiers from both armies, but the precise effect this has on colony population dynamics is unknown. One thing is clear however, there must be an overall gain of fighting.

### 6.3 A Partial Differential Equation Model

Although the Leslie matrix model gave some realistic results, it made use of potentially meaningless parameters and required massive computation to calculate the optimal reproductive strategies in each environment. Furthermore, since certain parameters were unknown, only a qualitative confirmation of the fighting hypothesis was possible.

Another popular method of modelling size-structured populations is to model size (and necessarily time) continuously, resulting in a partial differential equation model (see, for example, Metz and Diekmann, 1986; Sebens, 1987; Cushing, 1994). Typically such models examine the density of a population  $\rho(t, s)$  where  $t$  denotes time and  $s$  individual size, arriving at a partial differential equation of the form

$$\frac{\partial}{\partial t}\rho + \frac{\partial}{\partial s}(g\rho) = -d\rho, \quad (6.3)$$

where the functions  $g$  and  $d$  in (6.3) describe the relationship between an individual's size and its rate of change of size. Boundary conditions arise naturally from knowledge of the birth process, enabling in certain instances analytical solutions to be found.

#### 6.3.1 The Model

Consider three populations; a prey species and two rival predators who both compete and cannibalise one another. We make the following assumptions:

- In the absence of predators, prey grows logistically at rate  $r$  with carrying capacity  $K$ .
- Type  $i$  predators consume prey at rate  $\xi_i$ .
- A predator either grows, dies or divides in a short time interval
  - A type  $i$  predator of size  $x$  grows at rate  $G_i(x)$ ,
  - A type  $i$  predator of size  $x$  dies at rate  $\mu(x)$ ,
  - Predators collide and fight at rate  $\theta$ , the smaller predator dying, the larger maintaining the same size. (Thus the casualties suffered by the victorious larger colony are precisely offset by cannibalising the dead.)
  - Predators of type  $i$  reaching size  $a_i$  split in half forming two predators of size  $a_i/2$ .

Let  $n_i(t; x)$ ,  $i = 1, 2$ , denote the type  $i$  predator population at time  $t$ , so the number of type  $i$  predators between sizes  $x_1$  and  $x_2$  is

$$\int_{x_1}^{x_2} n_i(t; \eta) d\eta.$$

Let  $p(t)$  denote the prey population at time  $t$ . The assumptions stated above imply the prey population satisfies

$$\frac{dp}{dt} = rp(t) \left(1 - \frac{p(t)}{K}\right) - \xi_1 p(t) \int_{a_1/2}^{a_1} n_1(t; \eta) d\eta - \xi_2 p(t) \int_{a_2/2}^{a_2} n_2(t; \eta) d\eta. \quad (6.4)$$

Consider now the evolution of predator densities, and without loss of generality, consider only type 1 predators. Over a small interval of time  $\Delta t$ , colonies of type 1 will, if they avoid dying, grow by  $\Delta x$  where we demand

$$\frac{\Delta x}{\Delta t} = G_1(x). \quad (6.5)$$

Thus the above assumptions yield

$$n_1(t + \Delta t; x)\Delta x = n_1(t; x - \Delta x) \left\{ 1 - \mu(x - \Delta x)\Delta t - \theta\Delta t \int_{x-\Delta x}^{a_1} n_1(t; \eta)d\eta - \theta\Delta t \int_{x-\Delta x}^{a_2} n_2(t; \eta)d\eta \right\} \Delta x + \mathcal{O}(\Delta x). \quad (6.6)$$

Taking Taylor expansions of (6.6) about  $(t; x)$  and then limits as  $\Delta t \rightarrow 0$  yields the partial integrodifferential equation

$$\begin{aligned} \frac{\partial n_1}{\partial t}(t; x) + G_1(x) \frac{\partial n_1}{\partial x}(t; x) \\ + \left\{ \mu(x) + \theta \int_x^{a_1} n_1(t; \eta)d\eta + \theta \int_x^{a_2} n_2(t; \eta)d\eta \right\} n_1(t; x) = 0. \end{aligned} \quad (6.7)$$

Since predators growing to size  $a_1$  split in half producing two predators of size  $a_1/2$ , we have the boundary conditions

$$2n_1(t; a_1) = n_1(t; a_1/2). \quad (6.8)$$

Similarly, the type 2 predators satisfy

$$\begin{aligned} \frac{\partial n_2}{\partial t}(t; x) + G_2(x) \frac{\partial n_2}{\partial x}(t; x) \\ + \left\{ \mu(x) + \theta \int_x^{a_1} n_1(t; \eta)d\eta + \theta \int_x^{a_2} n_2(t; \eta)d\eta \right\} n_2(t; x) = 0 \end{aligned} \quad (6.9)$$

with boundary conditions

$$2n_2(t; a_2) = n_2(t; a_2/2). \quad (6.10)$$

The predator growth rates  $G_i$  relate to prey densities, a simple relation being

$$G_i(x) = \gamma_i \xi_i p(t) \quad i = 1, 2 \quad (6.11)$$

where  $\gamma_i$  denotes the efficiency at which a type  $i$  predator converts prey into growth.

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### 6.3. A PARTIAL DIFFERENTIAL EQUATION MODEL

For simplicity, we henceforth assume  $\mu$  and  $\theta$  are constants.

### 6.3.2 Optimal Colony Size

In the above model, at the single species equilibrium  $n^*(x)$ , equation (6.7) becomes the first order integrodifferential equation

$$0 = G \frac{dn^*}{dx} + \left\{ \mu + \theta \int_x^a n^*(\eta) d\eta \right\} n^*(x),$$

which upon rearranging gives rise to,

$$\frac{dn^*}{dx} = - \left\{ \frac{\mu + \theta \int_x^a n^*(\eta) d\eta}{G} \right\} n^*(x)$$

from which one obtains bounds on  $dn^*/dx$ ,

$$-\frac{\mu}{G} n^*(x) \geq \frac{dn^*}{dx} \geq - \left( \frac{\mu + \theta N^*}{G} \right) n^*(x). \quad (6.12)$$

Recall the function  $n^*$  satisfied the boundary condition  $2n^*(a) = n^*(a/2)$ . Upon defining the functions  $y(x)$  and  $z(x)$  to be the upper and lower bounds of  $dn^*/dx$  in (6.12) and considering their related boundary conditions, we get

$$\begin{aligned} \frac{dy}{dx} &= -\frac{\mu}{G} y(x) & 2y(a) &> y(a/2) \\ \frac{dz}{dx} &= -\frac{\mu + \theta N^*}{G} z(x) & 2z(a) &< z(a/2). \end{aligned}$$

Solving the ODE for  $z$  and applying the boundary conditions yields

$$2z(a) = 2A \exp \left\{ -\frac{\mu + \theta N^*}{G} a \right\} < z(a/2) = A \exp \left\{ -\frac{\mu + \theta N^*}{G} \frac{a}{2} \right\}$$

for some constant  $A$ , and upon rearranging gives

$$\ln 2 < \frac{\mu + \theta N^*}{G} \frac{a}{2}. \quad (6.13)$$



Similar treatment for the function  $y$  gives the inequality

$$\ln 2 > \frac{\mu a}{G/2}. \quad (6.14)$$

Combining inequalities (6.13) and (6.14) gives a lower bound for  $N^*$

$$0 < \left[ \ln 2 - \frac{\mu a}{2G} \right] \frac{2G}{a\theta} < N^*. \quad (6.15)$$

In the case of a single predator with split size  $a_1$ , the death rate of a colony of size  $x$  is

$$\mu + \theta \int_x^{a_1} n^*(\eta) d\eta,$$

from either non-fighting sources or from losing a fight. Suppose a mutation occurs in a single newly formed colony and the only difference between this mutated colony and the wild type from which it derived is that the mutated colony splits at a larger size  $a_2 = a_1 + \Delta a$ . When the size of this mutated colony is less than  $a_1$ , its death rate will be as above, but between sizes  $a_1$  and  $a_2$ , the death rate will just be  $\mu$  since there are no other colonies larger than  $a_1$  to which it can loose fights. The mutation takes a time  $t'$  to grow from size  $a_1/2$  to  $a_2$  where

$$t' = \frac{a_2 - \frac{a_1}{2}}{G}$$

and if it eventually splits, it must avoid dying during this period. The mutation will be selected for if and only if the probability it eventually gives birth exceeds  $1/2$ . To this end, define  $\Phi = \mathbb{P}[\text{avoid dying during } t']$ . Then if  $\Delta t$  is a small amount of time

and assuming colony death occurs via a Poisson process,

$$\begin{aligned}
\Phi &= \mathbb{P}[\text{avoid dying in } (0, \Delta t)] \times \mathbb{P}[\text{avoid dying in } (\Delta t, 2\Delta t)] \times \cdots \\
&\quad \cdots \times \mathbb{P}[\text{avoid dying in } (t' - \Delta t, t')] \\
&= \exp \left\{ - \left[ \mu + \theta \int_{a_1/2}^{a_1} n^*(\eta) d\eta \right] \Delta t \right\} \exp \left\{ - \left[ \mu + \theta \int_{a_1/2 + G\Delta t}^{a_1} n^*(\eta) d\eta \right] \Delta t \right\} \\
&\quad \cdots \exp \left\{ - \left[ \mu + \theta \int_{a_1 - G\Delta t}^{a_1} n^*(\eta) d\eta \right] \Delta t \right\} \exp \left\{ - \mu \frac{a_2 - a_1}{G} \right\} \\
&= \exp \left\{ \frac{\mu a_1}{2G} - \frac{\mu a_2}{G} - \theta \left[ \int_{a_1/2}^{a_1} n^*(\eta) d\eta + \int_{a_1/2 + G\Delta t}^{a_1} n^*(\eta) d\eta + \cdots \right. \right. \\
&\quad \left. \left. \cdots + \int_{a_1 - G\Delta t}^{a_1} n^*(\eta) d\eta \right] \Delta t \right\}
\end{aligned}$$

and there are  $a_1/2G\Delta t$  integrals in the square brackets, each bounded by  $N^*$ . Thus  $\Phi$  is bounded by

$$\Phi_l \equiv \exp \left\{ \frac{a_1 \mu}{2G} - \frac{a_2 \mu}{G} - \frac{a_1 \theta N^*}{2G} \right\} < \Phi < \exp \left\{ \frac{\mu a_1}{2G} - \frac{\mu a_2}{G} \right\} \equiv \Phi_u. \quad (6.16)$$

From these bounds on  $\Phi$ , we obtain the following results:

- (i)  $\Phi > 1/2 \Leftrightarrow$  type-2 invades
- (ii)  $\Phi_l > 1/2 \Rightarrow$  type-2 invades
- (iii)  $\Phi_u < 1/2 \Rightarrow$  type-2 does not invade.

Upon setting  $a_2 = a_1 + \Delta a$  in (6.16) and applying (ii) and (iii) above, it is seen by examining the size of  $\Delta a$  that the maximum possible colony size is  $2G \ln 2 / \mu$ . Similarly, the largest of the lower bounds for maximum colony size is  $2G \ln 2 / \mu + \theta N^*$ . Hence the optimal colony size  $a_{opt}$  satisfies

$$a_{opt} \in \left( \frac{2G \ln 2}{\mu + \theta N^*}, \frac{2G \ln 2}{\mu} \right). \quad (6.17)$$

Notice these bounds may also be obtained directly from the inequalities (6.13) and

(6.14).

**Example:** *Eciton burchelli* and *Dorylus molestus*

As an example of the model, we consider the optimal colony size as predicted by (6.17) for *Dorylus molestus* and *Eciton burchelli* army ants. We first estimate the necessary parameters using subscripts  $E$  and  $D$  to denote *E. burchelli* and *D. molestus* respectively.

*E. burchelli* colonies number approximately three per square kilometre in their habitat, while *D. molestus* are about three times as abundant in theirs; thus we choose  $N_E^* = 3$  and  $N_D^* = 9$ . A *Dorylus molestus* colony typically collides and fights with other *Dorylus molestus* colonies between two to three times per year, and given a colony migrates about 25 times per year, with a probability of about 0.1, it will fight during a given migration; since  $N_D^* = 9$ , we choose  $\theta_D = 0.01$ . There have been no reported observations of *Eciton burchelli* colonies fighting, but fighting is certainly a possibility. For this reason, we choose  $\theta_E = 0.001$ , i.e. fights are an order less in *E. burchelli* than in *D. molestus*. During a single activity cycle, a *Dorylus molestus* colony grows on average by 150 000 workers, hence  $G_D = 1.5 \times 10^5$ . Likewise, since *E. burchelli* colonies typically grow by about 10 000 workers per cycle,  $G_E = 10^4$ . Finally, since *Eciton burchelli* colonies live on average for about 6 years, or sixty cycles, we choose  $\mu_E = 0.02$  and use the same value for *Dorylus molestus* colonies assuming that queen lifetime is similar between the two species.

Applying these parameters to (6.17) gives for *Eciton burchelli* a maximum colony size ranging from 600 000 to 700 000 workers and for *Dorylus molestus* a maximum colony size between 10 and 20 million workers. Field data on largest colony sizes lie within these bounds, Franks (1985) recorded a maximum colony size for *Eciton burchelli* as 650 000 workers and Gotwald (1995) estimated *Dorylus molestus* colonies to be as large as 20 million workers; the model is clearly in excellent agreement with the data – and so provides more evidence supporting the fight hypothesis.

### 6.3.3 Colony Density

It was shown above that given colony growth rates, colony density and an inclination to fight, different colony sizes were selected for in different environments. Here we demonstrate that given colony growth rates, colony size and an inclination to fight, different colony densities are selected for in different environments. Recall equation (6.12) which establishes bounds for  $dn^*/dx$  at the single-species equilibrium  $n^*(x)$ ,

$$-\frac{n^*(x)}{G}\mu \geq \frac{dn^*}{dx} \geq -\frac{n^*(x)}{G}(\mu + \theta N^*).$$

Integration of this inequality over  $[0, a]$  suggests that for a suitable choice of some constant  $A$ ,

$$A \exp \left\{ -\frac{\mu}{G}x \right\} \geq n^*(x) \geq A \exp \left\{ -\frac{\mu + \theta N^*}{G}x \right\}. \quad (6.18)$$

Hence, using (6.18), the integral  $\int_x^a n^* dx$  is bounded below by

$$\frac{AG}{\mu + \theta N^*} \left[ \exp \left( -\frac{\mu + \theta N^*}{G}x \right) - \exp \left( -\frac{\mu + \theta N^*}{G}a \right) \right] \quad (6.19a)$$

and is bounded above by

$$A \frac{G}{\mu} \left[ \exp \left( -\frac{\mu x}{G} \right) - \exp \left( -\frac{\mu a}{G} \right) \right]. \quad (6.19b)$$

It is then obvious from the bounds provided by (6.19) predator density satisfies

$$A \int_{a/2}^a \exp \left\{ -\frac{\mu x}{G} \right\} dx \geq N^* \geq A \int_{a/2}^a \exp \left\{ -\frac{\mu + \theta N^*}{G}x \right\} dx$$

and upon evaluating the integrals yields

$$\begin{aligned} \frac{GA}{\mu} \left[ \exp \left( -\frac{\mu a}{2G} \right) - \exp \left( -\frac{\mu a}{G} \right) \right] &\geq N^* \geq \\ \frac{AG}{\mu + \theta N^*} \left[ \exp \left( -\frac{\mu + \theta N^*}{G} \frac{a}{2} \right) - \exp \left( -\frac{\mu + \theta N^*}{G} a \right) \right] & \end{aligned} \quad (6.20)$$

Suppose fighting is rare; an assumption supported by field data. Taking a Taylor expansion of the lower bound in (6.20) yields

$$N^* \geq \frac{AG}{\mu} \left[ \exp\left(-\frac{\mu a}{2G}\right) - \exp\left(-\frac{\mu a}{G}\right) \right] \left\{ 1 - \theta N^* \left( \frac{1}{\mu} + \frac{1}{G} \right) \right\} + \mathcal{O}(\theta^2)$$

which upon rearranging gives a lower bound for  $N^*$ ,

$$N^* \left\{ 1 + \theta \left( \frac{1}{\mu} + \frac{1}{G} \right) \frac{AG}{\mu} \Omega \right\} \geq \frac{AG}{\mu} \Omega$$

where

$$\Omega := \exp\left(-\frac{\mu a}{2G}\right) - \exp\left(-\frac{\mu a}{G}\right).$$

Hence we can bound  $N^*$  above and below by combining the above inequalities

$$\frac{AG}{\mu} \Omega \geq N^* \geq \frac{\frac{AG}{\mu} \Omega}{\left\{ 1 + \theta \left( \frac{1}{\mu} + \frac{1}{G} \right) \frac{AG}{\mu} \Omega \right\}}. \quad (6.21)$$

## Results

Once again, the parameter values are chosen to reflect the field data for *D. molestus* and *E. burchelli* and are precisely those presented in the previous section. Bounds for  $N^*$  are calculated using (6.21) for a range of  $A$  and are presented in table 6.1.

Upon examining table 6.1 and comparing these results to those of section 6.3.2 and the field data, we see the parameter  $A$  should be of the order of  $10^{-5}$ . Notice also, the across all ranges of  $A$ , mean colony densities for *D. molestus* is an order greater than for *E. burchelli*.

### 6.3.4 Discussion of Partial Differential Equation Model

In section 6.3.2, equation (6.17) gave bounds for the optimal largest colony size in terms of certain environmental parameters. These bounds were seen to be in excellent quantitative agreement with the field data and confirms the earlier belief that fighting

$A$	<i>D. molestus</i>		<i>E. burchelli</i>	
	<i>Lower</i>	<i>Upper</i>	<i>Lower</i>	<i>Upper</i>
$10^{-7}$	0.1356	0.1455	0.0124	0.0124
$10^{-6}$	0.8422	1.455	0.1239	0.1247
$10^{-5}$	1.758	14.55	1.1738	1.247
$10^{-4}$	1.973	145.5	7.6809	12.47
$10^{-3}$	1.997	$1.455 \times 10^3$	17.24	124.7
$10^0$	2.000	$1.455 \times 10^6$	20.00	$1.247 \times 10^5$

Table 6.1: Bounds for  $N^*$ , colony density, dependent on the unknown parameter  $A$  as calculated by (6.21). Parameter values for *Dorylus molestus* are  $\mu = 0.02$ ,  $\theta = 0.01$ ,  $G = 1.5 \times 10^5$ ,  $a = 2 \times 10^7$ , and for *E. burchelli* are  $\mu = 0.02$ ,  $\theta = 0.001$ ,  $G = 10^4$ ,  $a = 6.5 \times 10^5$ , these values being consistent with the previous section.

selects for larger colony size. Later, in section 6.3.3, the distribution of colony sizes was estimated, dependent on some parameter  $A$ . By comparison to field data, this parameter was seen to be to order of  $10^{-5}$  which subsequently gives very tight bounds for predator densities. Moreover, using this estimate for  $A$ , one can place bounds on colony size distributions using (6.18) and this is a testable aspect of the model.

Despite the excellent quantitative agreement between this model and the field data, there are numerous aspects it cannot consider. For example, it was assumed for simplicity that colony growth rates were linear, while for *Eciton burchelli* at least, they are not (see Franks, 1985). Furthermore, the model assumed colonies reproduced by a process of binary fission; there is some disagreement in the literature over whether *Dorylus molestus* colonies adopt this strategy (e.g. compare Leroux, 1979; Gotwald, 1995). Despite these severe limitations, the model fitted the data well, suggesting the precise manner of certain processes (e.g. colony growth rates) is irrelevant.

A problem with this model, in common with that of section 6.2.1, was that a colony gained little by fighting; hence this model cannot explain why aggressiveness is favoured. For this reason,  $\theta$  was not varied between two rival phenotypes.

It is highly desirable to obtain complete solutions of the system described by (6.4), (6.7) and (6.9). Unsurprisingly, this is extremely hard; (6.7) is hyperbolic on its own, and numerical solution of such equations is current research material for numerical

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### 6.3. A PARTIAL DIFFERENTIAL EQUATION MODEL

analysts.

There remain unanswered questions surrounding the PDE model; for example, can the system be adapted to consider non-even splitting, or different fighting rules and rates between rival phenotypes? Also, the prey densities were completely ignored in the analysis, since at equilibrium they only influenced the colony growth rate  $G$ ; the prey densities will have a crucial influence on the full dynamical system, for example, whether an equilibrium can arise in the first instance.

Finally, one question that puzzles me greatly. The growth rate for *E. burchelli* is much less than *Dorylus molestus*, partly because the former adopts a fixed activity cycle and may be forced to spend time on a poor quality patch, while *Dorylus molestus*, having no such fixed cycle, will not stay on a poor habitat patch. The question arises then, why has a fixed activity cycle been selected for in *Eciton burchelli*? For example, why does the colony not spend a day or so exploring the area that is going to be home for the next few weeks?

## 6.4 Summary

In this chapter the African army ant *Dorylus molestus* was introduced and the differences between this species and *Eciton burchelli* were highlighted. The most noticeable difference related to colony size; *D. molestus* colonies are 40 times larger than *E. burchelli*. A possible reason for this was stated as the species willingness to fight other colonies upon collisions. This conjecture was tested via two mathematical models; a Leslie matrix model and a partial differential equation model.

For the Leslie matrix model, the population was divided into discrete size class. Time was modelled discretely, since this was most appropriate to the biology, and a description of the population at time  $t + 1$  was given in terms of the population at time  $t$ . Then, by examining how rival phenotypes fared against one another, the optimal strategy for a given environment was obtained. This computationally intensive problem is made easier by the use of property 6.1. It was seen that the optimum strategies for the two considered environments agreed with the field data; in particular,

the fighting hypothesis gained more support.

A partial differential equation model was subsequently developed in section 6.3. Here the population was described by a continuous variable measuring colony size. Examination of the PDE at the steady-state solution gave bounds on the population structure, which were subsequently used to obtain an optimal colony size and colony density. The optimal values predicted by this model were seen to be in excellent quantitative agreement with field data, and also gave more evidence in favour of the fighting hypothesis.



## Chapter 7

# Overview of Thesis

The conservation of species has been the common thread throughout this thesis. In particular, I have tried to use mathematics to help aid in assessing conservation programmes and in focusing attention on those species most at risk from extinction. I was especially concerned with the tropical army ant *Eciton burchelli*, since it is an important member of the tropical rain forest ecosystem and has been well studied in the field.

In chapter 2, I developed two models to examine the effect of habitat fragmentation on the army ant *Eciton burchelli*. The first model was an analytical patch occupancy model which was used to assess how the random removal of rain forest influenced the abundance of army ant colonies. It was seen through both a mean field approximation and an improved mean field approximation that there existed a critical amount of habitat which could be randomly removed before army ant persistence became impossible. A spatially explicit computer simulation was subsequently developed and using this model I considered how different strategies of forest harvesting affected the abundance of the army ants. This model demonstrated that spatial effects were very important in issues relating to extinctions of army ants.

In chapter 3, I considered how catastrophes, such as climatic events, may influence the persistence of army ant colonies in forest fragments. I initially derived expressions for the birth and death rates of *Eciton burchelli* colonies and subsequently applied

them to several models published in the literature. These models gave data such as the conditional probability distribution of colony numbers and the expected time to population extinction. It was seen that catastrophes had a massive influence on population dynamics and it is worrying to note that so few mathematical models and conservation programmes account for their effect.

In chapter 4, I considered habitat corridors, and in particular addressed a concern that corridors may encourage species extinctions rather than prevent them. Three models were developed; a spatially explicit computer simulation, a general Markov Chain model and a Stochastic Differential Equation model. Upon applying the dynamics of the army ant *Eciton burchelli* to each model, it was seen in all cases that corridors could either prolong or reduce the expected extinction time, and hence either reduce or encourage extinctions. This important result suggested that conservation corridors should be evaluated on a case by case basis.

Antbirds, a close associate of army ants, were the subject of chapter 5, and in particular the extinctions of certain antbirds on Barro Colorado Island. I constructed two analytical models to examine a hypothesis which claimed the extinctions on the island are being caused by higher predation rates. The first model was a simple heuristic model, useful for qualitative assessment only, while the second model was an energy-based mechanistic model and hence useful for quantitative assessment. Both models were seen to support the hypothesis and be in good agreement with the field data. The mechanistic model was subsequently used to demonstrate how loose territoriality in the antbirds may have evolved from exclusively defended territories.

In chapter 6, I compared the American army ant *Eciton burchelli* to the African army ant *Dorylus molestus* and considered why different colony characteristics had been selected in the different environments, in particular the differences in colony size. Using two models, one a discrete time size-structured population model and the other a continuous time size-structured model, it was demonstrated that colony collisions and fighting led to an arms race within *Dorylus molestus*, implying colony size was larger where colonies frequently fought one another, consistent with the field data available.

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## Appendix A

# Habitat fragmentation, percolation theory and the conservation of a keystone species

by Graeme Boswell, Nicholas Britton and Nigel Franks (1998)

Proceedings of the Royal Society of London B **265**(1409):1921–1925.

# Habitat fragmentation, percolation theory and the conservation of a keystone species

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Many species survive in specialized habitats. When these habitats are destroyed or fragmented the threat of extinction looms. In this paper, we use percolation theory to consider how an environment may fragment. We then develop a stochastic, spatially explicit, individual-based model to consider the effect of habitat fragmentation on a keystone species (the army ant *Eciton burchelli*) in a neotropical rainforest. The results suggest that species may become extinct even in huge reserves before their habitat is fully fragmented; this has important implications for conservation. We show that sustainable forest-harvesting strategies may not be as successful as is currently thought. We also suggest that habitat corridors, once thought of as the saviour for fragmented environments, may have a detrimental effect on population persistence.

**Keywords:** habitat fragmentation; habitat corridors; conservation; extinction; tropical rainforest; percolation theory

## 1. INTRODUCTION

The tropical rainforests are the most important ecosystems of all in terms of biodiversity (May 1990) and they are being destroyed at an increasing rate (Gradwohl & Greenberg 1988; Laurance & Bierregaard 1997). Because habitat destruction is the major cause of species extinction (Ehrlich & Ehrlich 1981; Wilson 1992; Lawton & May 1995), this is the greatest conservation crisis. There have been many studies on the effect of habitat loss for mammals, but there have been comparatively few studies for insects (but see Laurance & Bierregaard 1997). This lack of attention to invertebrates is surprising given that invertebrates are more species-diverse than vertebrates in tropical forests by several orders of magnitude (Fittkau & Klinge 1973; May 1990). Indeed, as far as we are aware, ours is the only work that provides long-term conservation guidelines for any of the tropical rainforest insect species (see also Partridge *et al.* 1996).

The army ant, *Eciton burchelli*, is a keystone species in certain neotropical rainforest ecosystems; many species of vertebrates and invertebrates associate with them and would surely face extinction if the army ants disappeared (Willis 1967, 1974; Willis & Oniki 1978; Ray & Andrews 1980; Stouffer & Bierregaard 1995). Their near-daily raids create a mosaic of habitat patches in different stages of ecological succession, therefore promoting species diversity (Franks 1982*a,b*). Moreover, in Central and South America 50 bird species 'professionally' follow army ant raids: they depend almost entirely on the ants to flush insect prey out of the leaf litter (Willis & Oniki 1978).

To understand the population dynamics of the army ants, we have developed a stochastic individual-based

model which deals with space explicitly. For other examples of individual-based models see DeAngelis & Gross (1992). Our model is stochastic in the sense that the movement of colonies is random and this in turn leads to a stochastic birth and death process (Nisbet & Gurney 1982; Renshaw 1993). The individual-based approach allows us to keep track of both individual colony size and the number of colonies. Owing to the nature of individual-based models, multiple realizations are necessary to examine the variance and sensitivity of the system. Our model strongly suggests that there are critical thresholds both in the size of habitat islands and in the number of degraded patches within such habitat islands, beyond which the population becomes extinct. Even with appeal to results from percolation theory, which deals with fragmentation under the random removal of sites (Stauffer 1985; With & Crist 1995), the results we obtain are both surprising and counterintuitive. Our approach enables us to question future management strategies, not only with regard to *Eciton burchelli* but for many other species exposed to habitat fragmentation. In particular, we will consider in general the cost and benefits of habitat corridors and their role in conservation.

## 2. NATURAL HISTORY

*Eciton burchelli* army ants live in colonies that can number in excess of 500 000 individuals (Schneirla 1971; Franks 1985). Their raids have a massive impact. In the course of a day's raiding, a single colony captures some 30 000 prey items, mainly other social insect species (Franks 1982*b*). These raids also flush out larger arthropods, some of which are quickly devoured by ant-following birds (Willis 1967, 1974; Willis & Oniki 1978; Stouffer & Bierregaard 1995). Colonies exhibit a 35-day

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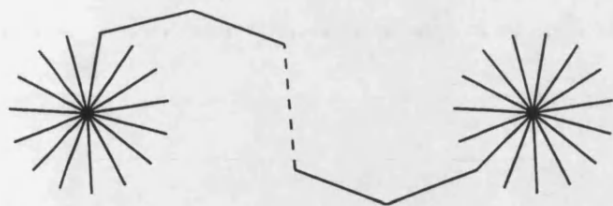


Figure 1. The raiding trails laid out during two statary phases and one intervening nomadic phase. The length of the raids are, on average, 90 m during the statary phase and 116 m during the nomadic phase. The mean direct distance migrated between two successive statary phases is 530 m (Willis 1967; Franks & Fletcher 1983).

activity cycle (Willis 1967; Schneirla 1971; Franks 1989). For 20 days, a colony resides in a fixed bivouac (nest) from which raids emerge nearly every other day (figure 1). During this so-called statary phase, the colony's single queen lays around 100 000 eggs (Rettenmeyer 1963; Franks 1985). At the end of the 20-day period, the eggs hatch into larvae and there are now more mouths to be fed so the raiding becomes more frequent and intense. The colony now enters the nomadic phase, where a new bivouac is formed at the end of each day's raiding trail (figure 1). This behaviour lasts for about 15 days, until the larvae pupate, and a new statary phase begins. At the end of each statary phase, the pupae become new callow workers (Schneirla 1971; Franks 1989).

Such 35-day cycles continue relentlessly through wet and dry seasons. Colonies die either through queen death or simply by the colonies becoming too small (Rettenmeyer 1963; Franks 1982b, 1985; Partridge *et al.* 1996). The largest colonies reproduce by rearing a sexual brood and then by splitting in half (Schneirla 1971). The daughter colonies are then headed either by the existing queen or by one of the new queens reared prior to the binary fission of the original colony (Franks & Hölldobler 1987).

### 3. THE MODEL

Our model is consistent with that of Britton *et al.* (1996) whereby we approximate the area raided by *Eciton burchelli* as a square of side 180 m, roughly the area raided during the statary phase. We assume the effects of nomadic-phase raiding are relatively small since the colony briefly passes through an area, rather than occupying it for a considerable time (figure 1). We model time discretely, one time-step representing the 35-day activity cycle. Thus we are dealing with a discrete-time stochastic cellular automata model, also known as a patch-occupancy model (Durrett & Levin 1994; Rand & Wilson 1995). For our simulations, we chose the habitable world to be 2500 patches (i.e. 50 cells  $\times$  50 cells, or an area of rainforest 9 km  $\times$  9 km). A number of patches are then randomly removed from the lattice, with reflecting boundary conditions imposed on these patches and on the edge of the lattice. The system is then allowed to change subject to several transition rules.

1. Each colony chooses to move to any of the 24 patches at the edge of a  $7 \times 7$  square, the centre of which is the current position (Britton *et al.* 1996). This fixes the distance a colony moves and is roughly equal to 530 m,

the direct overland distance between successive statary bivouacs (Willis 1967; Franks & Fletcher 1983). Hence, a colony can move from one square to any of the eight adjacent cells. Movement rules such as these have been used in numerous other models (Durrett & Levin 1994; Dytham 1995; Travis & Dytham 1998).

2. It moves in that direction until it hits a removed patch or the edge of the lattice at which point it reflects, like a beam of light reflected by a mirror.
3. The colony stops moving when it has migrated the distance determined in step 1.

When a colony moves onto a young patch, one that has recently been occupied and depleted of prey, it decreases in size, whereas when it lands on an old patch with plenty of prey, it increases in size. This approach is used to emulate the time it takes for an area of land to recover from the effects of raiding by army ants (Partridge *et al.* 1996). A maximum colony size is introduced and any colony exceeding this size splits into two colonies of equal size. This mimics natural behaviour (Franks 1985; Franks & Hölldobler 1987).

The reflecting boundary conditions imposed on the removed patches are consistent with observations made in Panama and elsewhere, whereby *Eciton burchelli* colonies do not move for a prolonged time into areas that have no canopy cover (Willis & Oniki 1978; Stouffer & Bierregaard 1995; N. R. Franks, personal observations).

We define a young patch to be one that has been occupied in the last six time steps (because patch recovery time is 200 days (Franks 1982b), a time step is 35 days and  $200/35$  is approximately six). Queen death is included and is assumed to occur via a Poisson process. Therefore, with probability  $1/(Q \times (365/35))$  the queen, and hence the entire colony, would die during the time-step,  $Q$  being the queen's average lifespan in years (Partridge *et al.* 1996). We took  $Q=6$ , a not unreasonable figure (Franks 1985).

Several simulations were conducted with various numbers of removed patches, the average number of colonies only being recorded once the system had settled down to a quasi-steady state (figure 2a).

### 4. RESULTS

Our simulations yield some surprising results, particularly highlighting the importance of habitat accessibility. As the proportion of randomly removed patches approaches 0.45, the number of colonies approaches zero, i.e. extinction (figure 2a). What is surprising here is that extinction occurs well before the lattice is broken up into separate clusters.

Percolation theory predicts that for an infinite lattice there is a critical percolation value where the expected cluster size goes from being infinite to being finite. A finite lattice having a finite cluster size will simply smooth this transition (figure 3). Extinction is to be expected for values above this phase transition value since none of the clusters of the fragmented space would support even one colony at equilibrium. For our choice of neighbourhood—eight adjacent cells—this critical value occurs when 0.5928 of the cells have been randomly removed (Stauffer 1985). (Note, for nearest-neighbour models—the four

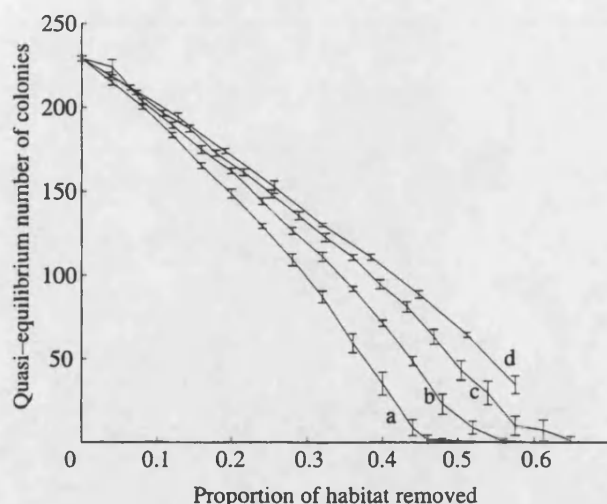


Figure 2. A proportion of habitat is randomly destroyed starting from 0 and changing in small increments (typically 0.04). One-tenth of the remaining habitat is then populated by colonies and the simulation is allowed to run for 500 cycles with only the last 300 iterations being recorded; this allows a quasi-steady state to be reached. The habitat is removed in various ways, (a)  $1 \times 1$  blocks, (b)  $2 \times 2$  non-overlapping blocks, (c)  $3 \times 3$  non-overlapping blocks and (d)  $4 \times 4$  non-overlapping blocks. Each such simulation is repeated ten times and the mean and standard deviation is shown. In (d) it becomes impossible to remove a  $4 \times 4$  block once a certain amount of habitat is removed because the remaining habitat is of such a complex shape that it rarely contains a single block of that shape (see also figure 5). In (a), a linear decline in colony numbers is to be expected since we are not close to the critical percolation value.

closest cells—the critical value is 0.4072.) Our results show that, unexpectedly, the populations go extinct well before this threshold. We repeated the simulation using a hexagonal lattice (G. P. Boswell, unpublished data) and observed the same pattern, namely the critical extinction-causing threshold of habitat removed was significantly less than the critical percolation value.

This phenomenon occurs because even though it is not impossible for a colony to get from one site in the cluster to any other, it may be very difficult (figures 4 and 5a). Hence a colony will predominantly occupy a region of a cluster and not necessarily the whole cluster. So a habitat that appears to be continuous may be unable to support a population of *Eciton burchelli*. One way of emphasizing this finding is to remove 0.45 of the habitat as a single block and leave the remaining habitat as a single large square. This will be able to support 100 colonies almost indefinitely (Britton *et al.* 1996; Partridge *et al.* 1996).

From this perspective, it would be better to remove large square clumps of forest than long strips to lessen the fragmentation. We tested this prediction by removing the habitat as non-overlapping blocks consisting of  $2 \times 2$ ,  $3 \times 3$  and  $4 \times 4$  patches, although the blocks themselves are still removed at random (figure 5). By removing habitat as progressively larger blocks, the degree of fragmentation decreases and the army ants' ability to persist increases (figure 2). For example, by removing 50% of the habitat as single patches, persistence is impossible. However, if the same amount of habitat is removed, but as  $4 \times 4$

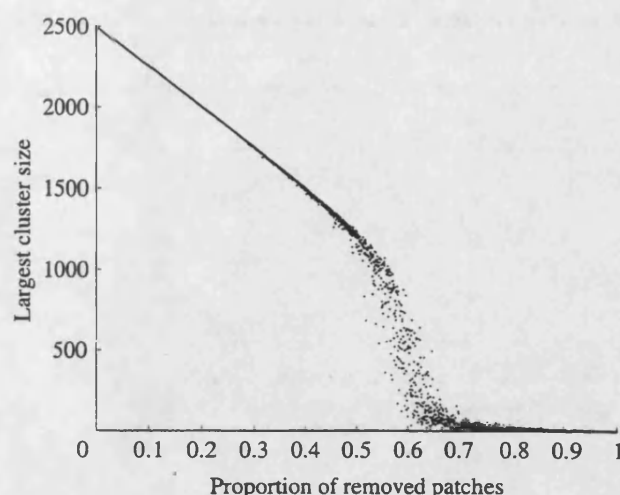


Figure 3. The size of the largest remaining cluster plotted as a function of the fraction of patches removed (where patches are removed totally at random). Two patches are neighbours of one another, and hence in the same clusters in the sense of nearest and next-nearest neighbours. Notice that even when half the patches are removed, the lattice still often consists of just one cluster or one large and a few very small clusters. (Hence it is possible to get from almost any one habitable patch to almost any other habitable patch.) In fact, the critical percolation value in this instance occurs when 0.4072 of the patches exist, i.e. when 0.5928 are removed (Stauffer 1985).

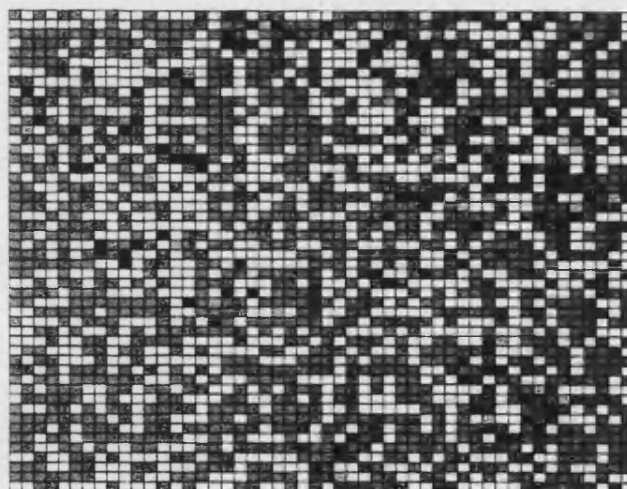


Figure 4. A snapshot of the lattice with 1000 patches removed. The red squares are those patches currently occupied: the darker the shade, the larger the colony. The white squares represent the removed patches. The blue squares are the young patches: the darker the shading, the more recent the raiding. The green squares represent the old patches, recovered forest. Finally, notice that the lattice basically consists of a single cluster, but is not far short of completely fragmenting.

blocks, some 70 colonies are able to persist at the quasi-steady state.

## 5. DISCUSSION

The importance of these results can be seen when one considers so-called sustainable forest management

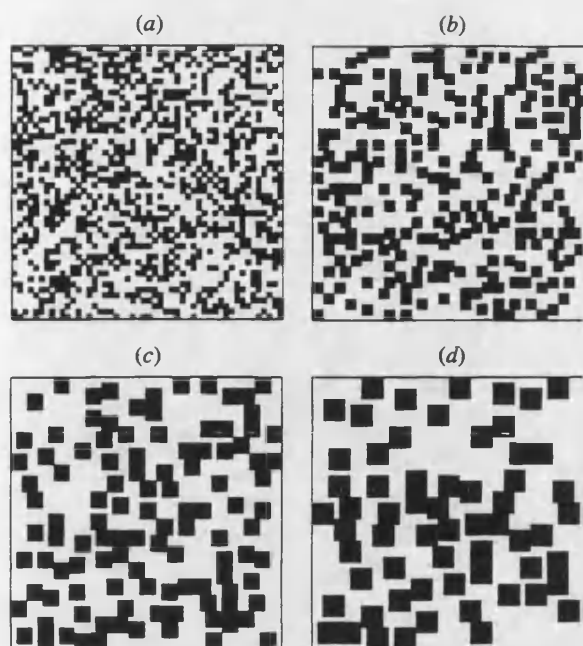


Figure 5. The effect of 'randomly' removing 40% of the habitat from a  $50 \times 50$  lattice. The black patches represent the removed habitat; the white patches represent forested areas. (a) The patches are removed totally at random. (b) The patches are removed in blocks of four patches (i.e.  $2 \times 2$ ). (c) The patches are removed in blocks of  $3 \times 3$ . (d) Patches removed in blocks of  $4 \times 4$ .

strategies, which involve felling long strips of woodland (Hartshorn 1989, 1995) so that a large forest is broken up into strips. These forested strips are internally fragmented by streams, roads, tree-fall gaps, etc., so that the actual cluster size may be a great deal smaller than one might be first led to believe. Our simulations predict that if the clusters are too small, or too inaccessible, then (at the very least) the army ant *Eciton burchelli* will become locally extinct.

A number of other authors have examined the effect of habitat removal on population persistence (Dytham 1995; With & Crist 1995; Bascompte & Solé 1996). For example, Dytham (1995) examined the effect of habitat removal on two interacting populations but did not interpret his results using percolation theory. He investigated how two species in competition fared in a fragmented environment where one was a superior disperser. His neighbourhood rules were the same as ours, namely direct movement into the eight adjacent cells. The poorer disperser went extinct while the habitat was still connected; the better disperser persisted until the percolation critical value was achieved, at which point there was a sudden shift in the abundance of this species. These results are entirely to be expected with the use of percolation theory (see also With & Crist 1995; Bascompte & Solé 1996).

Our results suggest that a better sustainable forest-harvesting strategy is to remove reasonably large square-like clumps. Of course, this is a very one-sided view. It is going to take less time for the forest to recover if felling is in the form of a long strip than a square clump. However, the value of faster recovery would be diminished because it would involve a cost: species reduction.

These results also raise questions about habitat corridors between reserves. For species that possess no 'long-term memory', that is to say they do not remember how they arrived at some point in space—as is the case for army ants—corridors between reserves have to be sufficiently large so that first the corridors can be found, and second they can be negotiated successfully. It is hard to lay down any figures on minimum corridor size, since differently shaped lattices and different models for local movements will yield different answers. However, these results certainly suggest that there is a minimum corridor width between small reserves to ensure the persistence of a population, because we observed persistence to be impossible if pockets of habitat are hard to find.

We have seen that geometrically complicated reserves are of little use to this keystone species: a colony becomes trapped in a small pocket of rainforest, depleting its local resources and thus facing starvation. It could be possible for this situation to be repeated in a habitat corridor and an individual (with poor or no navigational skills) enters a corridor, wanders back and forth, depleting its resources, and therefore leading to starvation. Given that the characteristics of habitat corridors are species-specific (Hobbs 1992), we could design a corridor that would suit one species but might be detrimental to others. In other words, habitat corridors may not be a solution to species loss through fragmentation, but could escalate the problem further. We are currently investigating this possibility.

Of course the equilibrium number of colonies does not tell the whole story. Almost surely any population will eventually become extinct (MacArthur & Wilson 1967; Mangel & Tier 1994). However, the time to extinction depends very strongly on the equilibrium number of colonies (Partridge *et al.* 1996), and this emphasizes the importance of not allowing the equilibrium number of colonies to fall too low.

We conclude that any future strategy for tropical rainforest management is going to have to take a great many issues on board: to look not only at short-term solutions but at more long-term effects as well. Conservationists must examine the trade-off between quicker forest recovery and an increased risk of extinction of certain species.

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## Appendix B

# Habitat fragmentation and swarm-raiding army ants

by Graeme Boswell, Nigel Franks and Nicholas Britton

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## INTRODUCTION

Different species have different habitat requirements and so viewed on the correct spatial scale the distribution of all species is patchy (Andrewartha and Birch 1954). This habitat patchiness can take quite dramatic forms such as fragmented forests or mountain tops, or can be as simple as leaves on plants. When these patches are totally disconnected, so that there is no flow of individuals between them, the population dynamics in one region will have no effect on the dynamics in other regions, so a species becoming extinct in one habitat patch will not affect extinction of that species in any other patch. However, when habitat patches have some degree of connectedness, the between-patch dynamics will play an important role (Hanski and Gilpin 1991). This is essentially what metapopulation dynamics is all about.

Imagine small islands in a lake, all relatively near to one another. Suppose a particular plant is introduced to one of these islands. Eventually, once the plant is well established, it will release seeds which give rise to daughter plants. Assume these seeds are wind dispersed. Some of the seeds remain on the island, some end up in the water but a few make it to neighbouring uncolonised islands. Once these few lucky seeds have germinated and new plants are established, they too may contribute to the colonisation of other islands. Of course, each plant has a chance of dying and it is the balance between the death rate and colonisation rate that will cause the plant species either to persist or go extinct relative to our group of islands. Intuition suggests that persistence is possible only if the colonisation rate is greater than the death rate. Later we shall present a mathematical model to investigate this further (Box 1).

Metapopulation dynamics are not just confined to ecology, they can be used in many other fields of study, most noticeably the spread of infectious diseases (Grenfell and Harwood 1997). Here towns and cities represent islands, each island being in one of two states, namely susceptible or infected. An infected town may pass on the disease to its susceptible neighbours. At the same time the disease in other towns could die out, leaving us with the classic model of islands undergoing extinction and colonisation.

We might expect that the nearer the local extinction rate is to the colonisation rate, the rarer the species (or disease) becomes. It is important to note at this stage that even if a species is rare, it does not mean it has little or no environmental impact. As an example, consider the prickly pear cactus (*Opuntia*) in Queensland, Australia (Andrewartha and Birch 1954). Sometime around the turn of this century, somebody introduced *Opuntia* to Queensland. Within few years, this cactus covered approximately a quarter of a million square kilometres of potentially productive land. Farmers wanted this plant to be brought under control and so the prickly pear's natural enemy, a certain species of moth (*Cactoblastis cactorum*), was introduced in 1925. Within ten years the cactus had all but vanished. All that now remains are very remote groups of plants, tens of kilometres apart from one another. What is remarkable here however is that only on a very small percentage of the plants can one find the moth. The moth is extremely rare, yet without it, hundreds of square kilometres of land would again quickly be covered by cacti. The message one takes from this example is that even a very rare species can have massive impact on an ecosystem.

Army ants are another example of a rare species acting as a metapopulation which can have a major impact on an ecosystem. We must be particularly concerned for them as their natural habitat, the tropical rain forest, is being rapidly destroyed.

Tropical rain forests are the richest ecosystems on Earth. For example, when techniques were developed in the 1970s and 1980s for collecting insects in new ways from the canopies of tropical rain forest, estimates of the total inventory of the world's biodiversity shot upwards from about 5 million species to 15 million or perhaps even 30 million species (Erwin 1983; Erwin 1991; May 1990; Stork 1988; Stork 1993; Stork 1994). Most of this diversity is associated with the species richness of tropical rain forest trees. For example, a single 50 ha plot of rain forest on Barro Colorado Island in Panama (see later) is home to 186 species of trees (Hubbell and Foster 1983). Compare this with the estimated 35 native species of trees in the whole of the British Isles (Mitchell 1974, p. 30).

The riches of tropical rain forest makes their destruction a greater crime. By the year 2000 approximately half of all of the tropical rain forest that graced this planet only a few centuries ago will have been cut (Laurance and Bierregaard 1997).

Almost everything about tropical rain forests is enigmatic. For example, they can be seen as immensely rich ecosystems living amidst potential deserts. Almost all the carbon and nutrients in these ecosystems is tied-up in living material. If large swathes of the forest are removed the soil is so poor that often long agricultural use is impossible and the forest is also unable to recover fully (Gradwohl and Greenberg 1988). Clearly nutrient recycling is important within tropical rain forest and the focal animals of this chapter, the army ants, are perhaps best seen as top predators of the detritivore food chain (Franks 1982a) which begins with leaves falling from the canopy of the forest and starting to decay in the leaf litter of the forest floor. As we will see in the next section even if just one species of army ant, *Eciton burchelli*, was to become extinct in the Neotropical rain forests of Central and South America - countless other species would ride with it on a one way journey to everlasting oblivion. Local extinctions of such species are ever more likely.

Conservation biology in the tropical rain forest has largely become the study of "Tropical Forest Remnants" to quote the title of a recent book edited by Laurance and Bierregaard (1997). Their use of the term remnants is appropriately redolent of the carnage we have wrought on these ecosystems. The remnant bits of tropical rain forest will be like so many tattered rags that remain after a pan-tropical jumble sale of the world's greatest biodiversity. We face the prospect of trying to rescue the few soiled and ragged fragments of what was once an immense natural richness. These remnants are likely to be all that remains to remind ourselves of our own relentless greed and short-sightedness. We could shrug our shoulders and try to avert our eyes from the problem or we could attempt some form of rescue. This chapter is devoted to the conservation of one magnificent predator in the rain forests of the neotropics. If we learn to preserve it and take the appropriate steps countless other species are sure to benefit.

## A DAY IN THE LIFE OF AN ARMY ANT

Contrary to myth and legend army ants are not just specialists in carnage, they can be helpful to other animals and can be extremely obliging creatures for study (Franks 1989; Gotwald 1995). Their savage raids can maintain diversity (Franks and Bossert 1983) and for a scientist interested in predator-prey interactions, they are in some ways surprisingly easy to study (Partridge et al. 1996). For example, one can stand within a few centimetres of an army ant raid and they will continue their activities oblivious. This means that they can be studied in quantitative detail

as they go about their business, undisturbed, in their natural habitat. Moreover, one can sit next to the column of ants returning from the swarm raid to the nest (Fig. 1(c)), or bivouac, and count all the 30,000, or more, prey items (mostly ants, cockroaches, spiders, scorpions) that they capture in a single day (Franks 1982b). It is the equivalent of being able to sit, unnoticed, in the throat of a large carnivore and count all of the food it swallows piece by piece. Moreover, because one can watch them wherever they go, it is also comparatively easy to record the spatial and temporal patterns of their raids (Franks and Fletcher 1983).

The best studied army ant population is that of *Eciton burchelli* in the lush lowland tropical forest of Barro Colorado Island, Panama (Fig. 1(f),(j)). This population was studied by T.C. Schneirla from the late 1920's through to the 1950's (Schneirla 1971), by Carl Rettenmeyer in the 1960's (Rettenmeyer 1963), by Ed Willis in conjunction with his investigations of the ant-following birds, also in the 1960's (Willis 1967) and by Nigel R. Franks and his colleagues starting in the late 1970's (Franks 1989). As a result of such work we know that there have been roughly 50 colonies inhabiting the 15 square kilometres of Barro Colorado Island throughout this time (Franks 1982c). For an invertebrate this is an exceptionally low natural density. Even though colonies may contain 500,000 workers (Franks 1985) they have only one queen. Hence, there are only about 3 reproductive individuals per square kilometre. *Eciton burchelli* colonies are rare. Even an experienced observer may take several days tramping the trails of Barro Colorado Island to find a single colony (Franks 1982c). Discovering a raid is, however, worth all the effort. The biggest raids sweep out an area 200m long by 20m wide in a single day (Franks 1985). Such is the density of raiding army ants at the swarm front that the leaf litter through which they raid is almost completely engulfed in the viscous flow of their dark writhing bodies (Fig. 1(b),(d)).

The colonies live to a 35 day rhythm. For 20 days they raid out from a single "statory" bivouac site like the spokes of an immense wheel. For the following 15 days they become nomadic and raid every day and emigrate down that raid path to a new foraging area almost every night (Fig. 1(e)). These alternating nomadic and statary phases continue relentlessly throughout the whole life of each colony (Schneirla 1971). They keep precisely to 35 days because their activity cycles are associated with the timing of brood production. In the middle of the 20 day statary period the single queen lays 100,000 eggs. Their embryonic development takes 10 days. When these eggs synchronously hatch into larvae the colony becomes nomadic. So like a good Napoleonic army, the ant army marches on its (social) stomach; the immense single cohort of larvae. The massive food requirements of these larvae explain why the colonies raid every day in the nomadic phase and must find a completely new area to raid every day. These larvae, because they are the same age, terminate their growth and spin their pupal cases in synchrony. This triggers the next statary phase. Pupal development takes 20 days so that the pupae hatch into new workers, ready to march into the next nomadic phase, just as the next cohort of eggs hatch triggering that nomadic phase. The beauty of the 35 day activity cycles is that during the statary phase the colony has no brood to feed. The colony can remain in the same bivouac site during the time the queen is vulnerably swollen with eggs and the colony can take a holiday from raiding every other day throughout the statary period.

Colony growth is slow, because colonies lose large numbers of workers through raiding casualties every 35 days (Franks and Partridge 1993). Approximately 1/3 of the colonies, i.e. the biggest ones, become reproductive each year (Franks 1985). They still maintain a 35 day cycle but instead of rearing just workers they rear 4,000 males and six queens (Franks 1985). Such

colonies reproduce in a process of binary fission, the new queens competing with one another and the old queen to head the daughter colonies (Franks and Hölldobler 1987). Outbreeding is probably the rule because males fly off to mate with queens in other colonies. The queens are never winged and hence colonies cannot invade new islands of habitat that are isolated by water or inhospitable terrain. However, because the males are strong flyers, isolated populations of colonies are not necessarily genetically isolated and therefore inbreeding in otherwise moderately isolated small populations is probably of little importance. Queens may live 6 years and during this time they will lay about 2 million eggs and walk 63 kilometres between bivouac sites (Franks 1989).

The local impact of raids is immense and because raided areas are slow to recover (Franks 1982b; Partridge et al. 1996), their impact on the tropical rain forest leaf litter fauna overall is massive even though army ant colonies are rare. Franks and Bossert (1983) estimated that about half of the area of Barro Colorado Island is still recovering from an *Eciton burchelli* army ant raid at any one time. The social insect prey, mostly other ants, being less mobile than the other arthropods that the army ants eat, are slowest to recover (Franks and Bossert 1983). Some of these prey ant species appear to be competitively dominant and other ant species can take advantage of their absence or low density in recently raided areas. It is in this way that army ants maintain diversity (Franks and Bossert 1983). In addition overall throughout Central and South America about 50 species of birds rely on the army ants' raids, to flush their prey out of the leaf litter (Fig. 1(a),(b)) and would probably go extinct in their absence (Willis and Oniki 1978). Countless species of invertebrate "camp followers" of the army ants would also become extinct following the demise of these wonderful Huns and Tartars of the insect world (Franks 1989; Hölldobler and Wilson 1990).

In sum, army ant colonies are the Bengal tigers of the insect world. They are rare and magnificent in their own right, and their ecological impact as keystone top predators in the tropical rain forest means they should occupy the first rank as subjects for conservation.

## THE ROLE OF MATHEMATICS IN CONSERVATION BIOLOGY

Conservation biology is about understanding how an ecosystem works, how species in it interact with, and how they depend on, one another. This means that when one species is threatened, for example through habitat loss, we, as conservation biologists, may be able to step in to minimise the overall damage. Mathematical models can help provide guidelines for such damage limitation. They can make qualitative and quantitative predictions, both in the long and short term, as to how an ecosystem will behave. We need long term predictions; it is not enough to know that species in a reserve will exist for the next five or ten years, we need to know if they are likely to exist in several hundred years time. Mathematics is the only way to extrapolate into the distant future with any hope of predictive power.

The modelling also serves a second purpose, namely it can suggest new experiments to be conducted in the field. This will yield more data and better insights which in turn can be used to refine the model which will lead to better experiments and analyses and so on. So, as we repeat such cycles of investigation, we will obtain better knowledge of the system, better models and so better conservation strategies.

Army ants would appear at first to be an incredibly hard system to model. However, because so much is known about their behaviour, the modelling is not as difficult as one might first imagine. This knowledge enables us to judge which features of the enormously complex biological system we can neglect and which we must include. That is, it helps us to determine the essential requirements for army ant persistence.

### Box 1. A simple metapopulation model

Suppose we have a series of patches that can be in one of two states, either occupied or unoccupied by a certain species. Suppose that this species colonises patches at a constant rate  $c$  and that occupied patches become empty (that is the population on this patch dies) at a constant rate  $m$ . Let us write  $p$  to represent the proportion of occupied patches. Then the rate at which empty patches are colonised is given by  $cp(1 - p)$ , since there are  $p$  patches from which the colonisation can occur and  $1 - p$  patches available for colonisation. Occupied patches become empty at a rate  $mp$ , since each occupied patch has death rate  $m$ . Thus we have the following equation describing how the metapopulation changes over time,

$$\frac{dp}{dt} = cp(1 - p) - mp.$$

This model is due to Levins (1969). We are interested in the model's steady states, since this is precisely when the metapopulation's size will be constant. That is we wish to solve the system with  $dp/dt = 0$ . Writing  $p^*$  as the solution at the steady state,

$$p^* = \begin{cases} 1 - \frac{m}{c} & \text{if } c > m \\ 0 & \text{if } c \leq m \end{cases}$$

We see that provided the colonisation rate exceeds the mortality rate, persistence is guaranteed and that the species is rare if  $m$  is nearly as high as  $c$ . It is possible to extend this model to include predator-prey interactions or multi-species competition simply by increasing the number of equations (Sabelis et al. 1991; Tilman et al. 1994). It is also possible to extend it to a system as complex as the army ant one by including size classes of colonies and recovery rates of raided patches in the model (Britton, Partridge, and Franks 1996). It turns out that these models describe the behaviour of real populations reasonably well (Hanski et al. 1994; Holyoak and Lawler 1996).

## A mathematical model for army ant dynamics

As Alan Turing said in 1952, a model is "a simplification and an idealisation, and consequently a falsification". The aim of mathematical modelling is *not* to obtain a system of equations that reflects a natural phenomenon as closely as possible, but to obtain one that is sufficiently complex to reflect the essential features of the phenomenon while being sufficiently simple to allow important general principles to emerge. For example, it is often *better* to use a Newtonian model of dynamics than a relativistic one. The art of mathematical modelling is in deciding what can safely be omitted.

Since the biology of army ants is so well known, this omission becomes a process of careful abstraction. The habitat consists of a series of patches. During the nomadic phase, a colony will travel through many different patches and so provided the numbers of good and bad patches are the same, the nomadic phase, for the purposes of modelling, can be considered to make minimal contribution to changes in colony size. Also, since raids during the nomadic phase only briefly pass through an area, rather than occupy it for a prolonged time, the recovery of patches from nomadic raids become negligible compared to recovery from statary raids. We conclude that the nomadic phase can safely be omitted and we are left considering purely the statary phase. Thus we consider a patch-occupancy model (Caswell and Etter 1993).

Hence, some features of army ant dynamics that we consider essential are as follows.

- The habitat is a mosaic of patches in different stages of ecological succession.
- A colony becomes larger if it spends its statary phase on a good patch, smaller if it spends it on a bad patch.
- A colony undergoes fission if it becomes sufficiently large.
- A colony dies if it becomes too small.
- A colony dies if its queen dies.

We model the patches as squares whose size is a typical area exploited by a colony in a statary phase, and whose status (good or bad) depends on how long it is since the patch was last exploited. At each time step, equal to the time for one activity cycle, each colony moves at random to a square at a distance typical of the species (Fig. 1(g)). It then increases or decreases in size by one size class, depending on whether the patch is good or bad, and may either split or die. The process is repeated indefinitely. The size of the patches, the time for recovery of an exploited patch, the distance moved in a nomadic phase, and the number of ants in a size class are parameters obtained from the biological data (Franks 1989). For more details see Britton et al. (1996).

The model as described is ideally suited to computer simulation and this reveals complex spatial patterns of extinction and re-colonisation of habitat patches, with the total number of colonies oscillating about a fixed level. However, it does not lead to expressions for the quantities of interest in terms of the parameters of the system, and we perform some mathematical analysis on a simplified model to achieve this. The first step is to apply the ideas of metapopulation theory outlined in Box 1. This gives a deterministic steady state about which the simulation model oscillates, but does not consider the stochastic variations that will eventually drive the population to extinction.

To do this, we think of the population as a gambler, with capital equal to the number of colonies it contains. It wins a toss every time a colony divides, and loses one every time a colony dies. But there is an upper limit on its capital, since there can never be more colonies than there are patches on the island. Hence the population is doomed to extinction, as stated in Box 2, and the only question is how long we might expect it to survive before this doom overtakes it. This time, in number of tosses, is determined as outlined in Box 2, for a game against an infinitely rich opponent. It is the expected time to extinction of the population. To convert it to a time in

years we need to know how frequently, on average, a coin is tossed, i.e. how frequently colonies divide or die. To do this we consider a colony newly formed by fission. It may be thought of as a second kind of gambler entering a new game with capital equal to the number of ants it contains. It gambles with these ants, a size class at a time, each time it exploits a new patch, winning the toss if the patch is good and losing it if the patch is bad. Eventually it wins the whole game, by becoming large enough to divide, or loses it, by dying. The expected duration of the game is determined as in Box 2, for a game against an opponent with finite funds, and leads to a determination of the expected time between tosses for the population game. The expected time to population extinction can then be calculated in years (Fig. 1(h)).

### Box 2. Gambler's ruin problems

The simplest problem of this sort is the following. Two gamblers start a coin-tossing game with a pool of  $\mathcal{L}N$  in cash, Janet having  $\mathcal{L}n$  and John  $\mathcal{L}(N - n)$ . At each toss of the coin Janet wins one pound from John if the coin falls heads, and John wins one pound from Janet if the coin falls tails. The probability that the coin falls heads is  $p$ , tails is  $q = 1 - p$ . The game ends when one of the gamblers loses all their money. Let the probability that Janet wins the whole game be  $P_n$ . Then by considering what happens after one toss it can be seen that

$$P_n = pP_{n+1} + qP_{n-1},$$

and it is clear that  $P_0 = 0$ ,  $P_N = 1$ . (Janet has lost the game if she has no money, but has won if she has all the money.) This is a simple set of equations to solve for  $P_n$ , and the solution is given by  $P_n = \frac{(q/p)^n - 1}{(q/p)^N - 1}$  if  $p \neq q$ ,  $P_n = \frac{n}{N}$  if  $p = q = \frac{1}{2}$ . Now let the expected time (number of tosses) that the game takes be given by  $T_n$ . Then, by a similar argument,

$$T_n = pT_{n+1} + qT_{n-1} + 1,$$

with  $T_0 = 0$ ,  $T_N = 0$ . (The game finishes immediately if Janet has no money or all the money.) Again these equations can be solved for  $T_n$ , and the solution is given by

$$T_n = \frac{n}{q-p} - \frac{N}{q-p} \frac{(q/p)^n - 1}{(q/p)^N - 1} \text{ if } p \neq q, \quad T_n = n(N - n) \text{ if } p = q = \frac{1}{2}.$$

We have assumed that  $p$  is constant. If this is not so, as in the army ant application, the problems may not have solutions that can be written in such simple forms, but the systems of equations can be solved on a computer.

A variation occurs if Janet again starts with  $\mathcal{L}n$ , but now plays against a bank with unlimited funds. Then the game can never end in a win for Janet, and must either go on indefinitely or end in her becoming bankrupt. If there is a fixed ceiling to her fortune, the probability that the game ends in her bankruptcy is 1.

## Habitat destruction and percolation theory

We shall now consider the problems that occur if some parts of the army ants' habitat are not easily accessible from other parts. The tropical rain forests are being destroyed at an increasingly alarming rate (Hartshorn 1995; Whitmore 1997). With habitat loss being the main cause of



species extinction (Lawton and May 1995), this is a major concern. Much of this destruction occurs through logging and as conservation biologists we wish to determine harvesting strategies that will have minimal impact on the rain forest ecosystem. One such proposed strategy has been to randomly fell strips of woodland comparable in area to the patches used in our mathematical model (Hartshorn 1989). This attempts to mimic naturally occurring tree-fall gaps and should allow for quicker recovery of the forest (Hubbell and Foster 1992). Here we will test how such management strategies may affect army ants and from this will be able to conclude several key conservational issues.

Due to the complex mathematics that would be involved, we have no choice but to resort to simulation on a computer. We consider an island containing 2500 patches, that is a reserve  $9\text{km} \times 9\text{km}$ . Then to observe the effects of habitat destruction we randomly remove some of these patches from the lattice. Since *Eciton burchelli* will not venture into unshaded areas for a prolonged time (Willis and Oniki 1978, N. R. Franks personal observations), these removed patches are truly uninhabitable.

Simulations were conducted for various numbers of removed patches with the average number of colonies being recorded only once the system had settled down (Fig. 2). We observed persistence to be impossible once 45% of the habitat had randomly been removed.

There is a branch of mathematics, known as percolation theory (see Box 3), which deals with how lattices behave under the random removal of sites (Fig. 1(i)). Using standard results from percolation theory (Stauffer 1985), we know that our lattice becomes truly fragmented only when about 60% of the habitat has been randomly removed. We discovered army ant persistence to be impossible when just 45% of the habitat patches were removed, but this occurs when the habitat is still connected. Compare this to the situation where 45% of the habitat is removed, but what remains is left as a large square – this should support on the order of 100 colonies for the island size considered (Britton et al. 1996). Thus, even if a large habitat is connected we cannot guarantee persistence.

The reason for this behaviour is surprisingly simple. If we randomly remove about 40–45% of the habitat, the remaining habitat still consists of just one connected cluster (Fig. 3). This cluster takes the form of lots of small habitat pockets connected to one another by narrow corridors (Fig. 1(i)). Each of these pockets is too small to support even one colony for a considerable time period (Partridge et al. 1996) and so any colony in such a pocket will need to leave pretty quick. Since the corridors are small (hence hard to find) and the ants do not remember how they arrived in the pocket in the first place, it is pure luck if they escape. However, if the colony is lucky and escapes from this pocket it will find itself in another pocket, facing the same problem. Again luck is its only hope for survival. At some point however, the colony's luck is going to run out and it will die.

This result is remarkable. The forest does not even have to be fragmented to cause major problems, it just has to be sufficiently difficult to get from one area to another. This has important implications for conservation.

### Box 3. Percolation theory

Imagine we have an infinite square grid, all the patches coloured white. Let's take a coin which has a probability  $p$  of coming up heads and probability  $q = 1 - p$  of coming up tails. For each square in our lattice we toss the coin; if it comes up heads (with probability  $p$ ) the square remains white whereas if it comes up tails (with probability  $q$ ) the square turns black (Fig. 1(i)). We now ask whether it is possible to get from any one white square to any other white square via some white "path". A path refers to how one is allowed to travel around the lattice; we may be allowed to travel only to the nearest neighbours or more complicated paths may be possible. Percolation theory is concerned with how  $p$  effects one's ability at being able to get from any one white square to any other white square via a path of white squares.

We can rephrase this slightly in terms of clusters and cluster sizes. Two white squares are said to be in the same cluster if there exists a white path between them. The size of a cluster is simply the number of white squares it contains. Now percolation theory is concerned with how  $p$  effects the average cluster size (see Fig. 3). It turns out that there is a critical percolation value  $p_c$  above which the mean cluster size is infinite and below which it is finite (Stauffer 1985).

For our purpose we define a path in the nearest and next-nearest neighbour sense, that is a colony can move straight to any of the eight surrounding patches during the course of its migration. In Fig. 3 we show that  $p_c \sim 0.4$  in this instance.

## COMPLICATIONS FOR CONSERVATION

### Harvesting strategies

Many sustainable forest harvesting strategies involve randomly felling strips of forest comparable in area to the square patches used in the model (Hartshorn 1989). We have seen that this approach may have severe consequences if the felling is too widespread, since breakages in the forest caused by harvesting combined with the natural breakages such as rivers and large tree-fall gaps, will begin to fragment the forest. This suggests that a better strategy would be to concentrate harvesting in a large square pocket of rain forest and systematically move onto other areas in order to lessen the fragmentation. Admittedly this does not take into consideration forest recovery, since small strips of forest will recover a lot quicker than large square clumps. Clearly, forest recovery will play an important role, since after just eight to ten years parts of the environment have recovered sufficiently in a forest fragmentation project near Manaus in Brazil for army ant inhabitation (Stauffer and Bierregaard 1995). However, since random felling increases the risk of species extinction, forest recovery rates will play a less important role in determining conservation strategies.

Clearly, as conservation biologists, we need to spend a great deal more time and effort in trying to understand the effects of heterogeneous habitats since the results can be totally counter-intuitive.

## Habitat corridors

It is widely believed that the establishment of habitat corridors between reserves will reduce a species' extinction risk (Hobbs 1992). This seems obvious – by increasing the area of a reserve we increase the number of individuals it contains and so increase the persistence time. We have seen previously, however, that even a very large reserve with poor internal connections is not sufficient for species persistence. Thus if the corridors are too small they will not allow movement of individuals between habitat pockets so that the corridor will not play a role in extending persistence times. We conclude from this that corridors have to be wide; how wide depends on the biology of the species under consideration. To determine this width we need to understand how a species locates a corridor, whether it will enter the corridor and then its subsequent behaviour in the corridor.

With regards army ants, corridors seem to be located by chance, so the entrance to the corridor ought to be reasonably wide. Once in the corridor, given how colonies move during the nomadic phase (one day's raid is in a similar direction to the previous), a narrow corridor would channel movement and speed up corridor passage (Tishendorf and Wissel 1997). So an ideal corridor would have wide entrances funnelling down to a narrow strip of woodland in the middle. This shape of corridor may well also suit the antbirds who are quite happy to follow raids of army ants wherever they may lead (Willis 1967; Stouffer and Bierregaard 1995). However, most habitat corridors are species specific (Hobbs 1992) and whilst the ants and ant-following birds might be content with such corridors, other associates may not. This is a real cause for concern. We must understand how *all* species in an ecosystem rely on one another before any effective conservation strategy can be implemented.

## Suitable reserves

When planning a reserve, the single most important figure to be taken into consideration is the expected time to extinction. This depends very strongly on the number of individuals a reserve can support (MacArthur and Wilson 1967). For example, a reserve so large that army ants would be expected to persist for 10000 years would need to contain at least seven colonies at equilibrium (Partridge et al. 1996). However, this figure only considers the ant colonies themselves and not any of the associated species, nor does it allow for catastrophes (see below). Certainly the antbirds will require a much larger reserve in which to function, since on Barro Colorado Island, Panama (Fig. 1(j)), which is seven times this size, about ten bird species (including one or two ant-following birds) were becoming extinct every decade (Willis and Oniki 1978) some 50 years after the reserve was isolated from the surrounding mainland.

Clearly, the relationship between army ants and their associates, in particular the ant-following birds, requires further investigation. Mathematics may well be the ideal tool for such studies.

## Role of catastrophes

Large reserves supporting many colonies will have long persistence times. For such reserves, the most likely cause of extinction will be catastrophes (Mangel and Tier 1994). These catastrophes may take several forms e.g. disease, forest fires or El-Niño induced events. With El-Niño events

becoming ever more frequent as we head to the end of the century (Wuethrich 1995), we need to understand how catastrophes influence the population dynamics of all species in order to prevent them from extinction. One thing is for certain, catastrophes can dramatically reduce the expected time to extinction and so any conservation plan must include their effects.

### **Concluding thoughts**

If army ants go extinct many other species will go extinct too. Conversely, if large viable populations of army ants can be conserved many other species will be conserved too. (Note however that Barro Colorado Island has viable army ant populations but not ant-following bird populations). Conserving army ants and their followers will need large tracts of continuous rain forest or even vastly larger tracts of forest fragments linked by broad corridors. It would be a distinct mistake to consider army ants as especially poor dispersers and hence particularly vulnerable to habitat patchiness. The ant-following birds for example will not cross more than a few metres of water and various tree species are known to be poor dispersers. Preserving what remains of the tropical rain forest will require expert studies both in field work and mathematical modelling in addition to a major change in the way we treat the natural world.

### **Acknowledgements**

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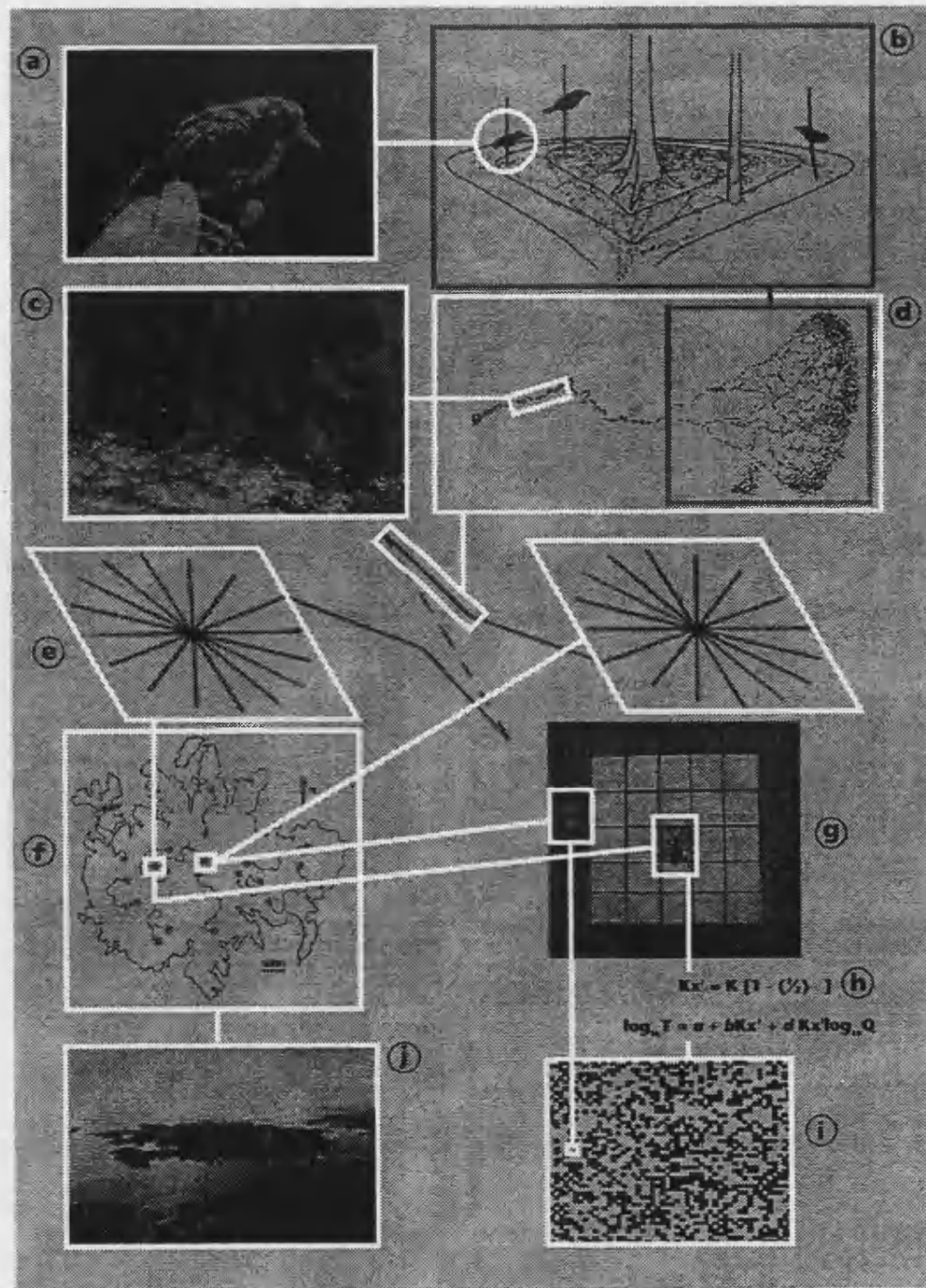


Figure 1: (a) A bicolored antbird (*Gymnopithys bicolor*). (b) How ant-following birds use swarms. Redrawn from Willis and Oniki (1978). (c) Some of the 30000 prey items returning to the nest. (d) A typical day's swarm raid. Redrawn from Rettenmeyer (1963). (e) Raiding patterns over two statary and one nomadic phase. (f) Map of Barro Colorado Island in Gatun Lake, Panama, showing some raiding trails drawn to scale. (g) A cellular automata model for the army ants. (h) Equations for mathematical model. The first describes the number of colonies in a reserve of size  $K$  patches.  $Kx^*$  denotes the number of colonies and  $n$  is the patch recovery time (in cycles). The second equation is the expected time to extinction.  $T$  is the expected time to extinction in years,  $Q$  expected queen lifetime and  $a, b$  and  $d$  are constants. (i) Percolation matrix with 40% of patches removed. (j) Barro Colorado Island.

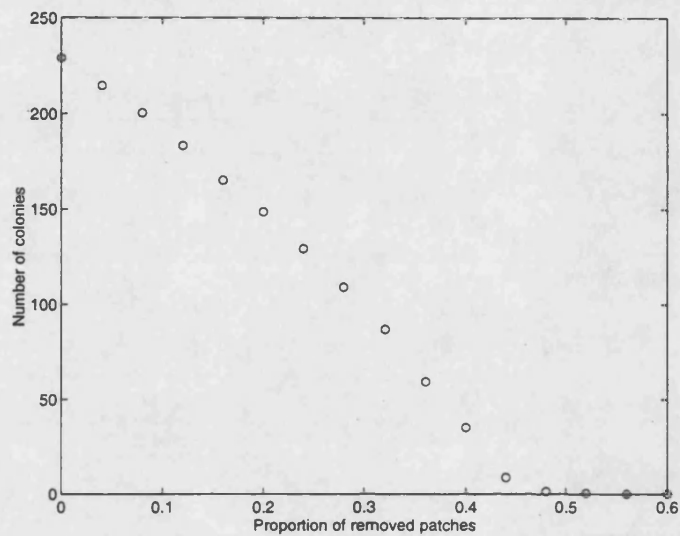


Figure 2: The average number of colonies as a function of the proportion of removed patches. Twenty simulations were conducted in each case for various numbers of removed patches from a  $50 \times 50$  lattice. The average number of colonies was recorded on each run only after the system had settled down to a quasi-steady state. (Quasi-steady since the only true steady state is extinction.) Notice that there is a transition from persistence to extinction when the proportion of removed patches reaches 0.45.

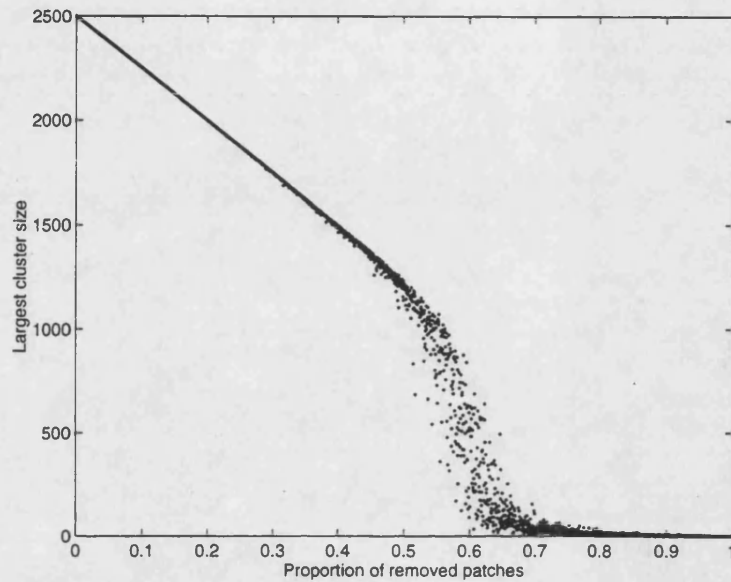


Figure 3: The size of the largest cluster is plotted as a function of the proportion of patches removed for a  $50 \times 50$  lattice. Each data point is the average of five runs, making the total number of runs 12500 ( $5 \times 50 \times 50$ ). Here patches are neighbours of one another in the sense of nearest and next-nearest neighbours. Notice that when less than 60% of the patches are removed the lattice consists of just one connected cluster with possibly a few isolated patches. When more than 60% are removed, we obtain many small clusters. This suggests that the critical percolation value occurs when about 60% of the patches are removed. In fact, the critical percolation value in this instance occurs when 59.28% of the patches are removed. See for other other examples Stauffer (1985).

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## Appendix C

# Alternative Heuristic Antbird Model

In this appendix we re-derive the simple antbird model of section 5.2 using a different mechanism for modelling competition — a logistic function rather than a negative exponential function. We make the same assumptions about antbird behaviour as before, and for convenience the parameter descriptions are repeated here.

Let  $N_t$  and  $M_t$  denote the number of adult females of the superior competitors and exploiters respectively in year  $t$ . Further parameters are given in table C. As in section 5.2, some conditions are enforced on the parameters

- $p_1 + p_2 \leq 1$  — there are three foraging scenarios
- $1 > r_1 > r_2 > 0$  for both  $N$  and  $M$  — ant swarms provide the best food source
- $r_2^M > r_2^N$  — allows competitive coexistence.

Parameter	Description
$K_N$ ( $K_M$ )	Carrying capacity of $N$ ( $M$ )
$\alpha_N$ ( $\alpha_M$ )	Annual female adult mortality rate for $N$ ( $M$ )
$\beta_N$ ( $\beta_M$ )	Female juvenile mortality rate for $N$ ( $M$ )
$n_N$ ( $n_M$ )	Maximum number of successful broods raised by a single $N$ ( $M$ ) per year in absence of predation
$p_1^N$ ( $p_1^M$ )	Proportion of time $N$ ( $M$ ) spends following swarms in own territory
$p_2^N$ ( $p_2^M$ )	Proportion of time $N$ ( $M$ ) spends following swarms in neighbouring territory
$r_1^N$ ( $r_1^M$ )	Relative amount of food found at neighbour's swarm by $N$ ( $M$ ) compared to own swarm
$r_2^N$ ( $r_2^M$ )	Relative amount of food found away from swarms by $N$ ( $M$ ) compared to own swarm
$c$	Strength of competition of $N$ over $M$

Table C.1: A description of the parameters used in the alternative derivation of the simple antbird model

### C.1 Two Competing Species Model

In a similar fashion as in section 5.2, the following difference equations are derived for the superior competitor and exploiter:

$$N_{t+1} = \left\{ (1 - \alpha_N) + (1 - \beta_N)n_N \times \left[ p_1^N + r_1^N \left( 1 - \frac{N_t}{K_N} \right) p_2^N + r_2^N (1 - p_1^N - p_2^N) \right] \right\} N_t, \quad (\text{C.1a})$$

$$M_{t+1} = \left\{ (1 - \alpha_M) \left( 1 - c \frac{N_t}{K_N} \right) + (1 - \beta_M)n_M \left[ p_1^M \left( 1 - c \frac{N_t}{K_N} \right) + r_1^M \left( 1 - \frac{M_t}{K_M} \right) \left( 1 - c \frac{N_t}{K_N} \right) p_2^M + r_2^M (1 - p_1^M - p_2^M) \right] \right\} M_t. \quad (\text{C.1b})$$

Notice the only difference between this revised model and the initial version (5.2,5.8) relates to the manner in which competition is modelled — here a logistic term is used for both intra- and inter-specific competition.

### C.1.1 Stability Analysis

The equilibria of the system described by (C.1) may be determined in a straightforward fashion. The steady states for  $N$  can easily be shown to be

$$N^* = 0 \quad (\text{C.2a})$$

and

$$N^* = K_N \left\{ 1 - \frac{1}{r_1^N p_2^N} \left( \frac{\alpha_N}{(1 - \beta_N)n_N} - p_1^N - r_2^N(1 - p_1^N - p_2^N) \right) \right\}. \quad (\text{C.2b})$$

The non-trivial steady state (C.2b) makes biological sense if, and only if,  $0 \leq N^* \leq K_N$ , i.e. precisely when

$$0 \leq \frac{1}{r_1^N p_2^N} \left[ \frac{\alpha_N}{(1 - \beta_N)n_N} - p_1^N - r_2^N(1 - p_1^N - p_2^N) \right] \leq 1$$

which upon rearranging yields the condition

$$\begin{aligned} (1 - \beta_N)n_N [p_1^N + r_2^N(1 - p_1^N - p_2^N)] &< \alpha_N \\ &< (1 - \beta_N)n_N [r_1^N p_2^N + p_1^N + r_2^N(1 - p_1^N - p_2^N)]. \end{aligned} \quad (\text{C.3})$$

We shall henceforth restrict our parameters to satisfy these inequalities, which is not as restrictive as first appears (see later).

Similarly, the steady states for  $M$  can be shown to be

$$M^* = 0 \quad (\text{C.4a})$$

and

$$\begin{aligned} M^* = K_M \left\{ 1 + \frac{1}{r_1^M (1 - c \frac{N^*}{K_N}) p_2^M} \left( \frac{(1 - \alpha_M) (1 - c \frac{N^*}{K_N})}{(1 - \beta_M)n_M} + p_1^M \left( 1 - c \frac{N^*}{K_N} \right) \right. \right. \\ \left. \left. + r_2^M(1 - p_1^M - p_2^M) \right) \right\}. \end{aligned} \quad (\text{C.4b})$$

This equilibrium is biologically meaningful if, and only if,  $M^* \in [0, K_M]$  which is easily shown to be equivalent to the condition

$$\begin{aligned} -r_1^M p_2^M \left(1 - c \frac{N^*}{K_N}\right) < \\ \frac{(1 - \alpha_M) \left(1 - c \frac{N^*}{K_N}\right)}{(1 - \beta_M) n_M} + p_1^M \left(1 - c \frac{N^*}{K_N}\right) + r_2^M (1 - p_1^M - p_2^M) < 0. \end{aligned} \quad (C.5)$$

Thus the system (C.1) has four equilibria, corresponding to coexistence,  $N$  only,  $M$  only or extinction. The stability of each of these steady states may be determined by the usual methods, i.e. by examining the Jacobian of the system:

$$J = \begin{pmatrix} \frac{\partial F}{\partial N} & \frac{\partial F}{\partial M} \\ \frac{\partial G}{\partial N} & \frac{\partial G}{\partial M} \end{pmatrix} \quad (C.6)$$

where the functions  $F$  and  $G$  are the right hand sides of (C.1a) and (C.1b) respectively. The elements of the Jacobian matrix are easily seen to be

$$\begin{aligned} \frac{\partial F}{\partial N} &= \left\{ (1 - \alpha_N) + (1 - \beta_N) n_N \left[ p_1^N + r_1^N \left(1 - \frac{N}{K_N}\right) p_2^N + r_2^N (1 - p_1^N - p_2^N) \right] \right\} \\ &\quad - (1 - \beta_N) n_N r_1^N p_2^N \frac{N}{K_N} \\ \frac{\partial F}{\partial M} &= 0 \\ \frac{\partial G}{\partial N} &= -c \frac{M}{K_M} \left\{ (1 - \alpha_M) + p_1^M n_M (1 - \beta_M) + r_1^M p_2^M \left(1 - \frac{M}{K_M}\right) (1 - \beta_M) n_M \right\} \\ \frac{\partial G}{\partial M} &= \left\{ (1 - \alpha_M) \left(1 - c \frac{N}{K_N}\right) + (1 - \beta_M) n_M \left[ p_1^M \left(1 - c \frac{N}{K_N}\right) \right. \right. \\ &\quad \left. \left. + r_1^M \left(1 - c \frac{N}{K_N}\right) \left(1 - \frac{M}{K_M}\right) p_2^M + r_2^M (1 - p_1^M - p_2^M) \right] \right\} \\ &\quad - (1 - \beta_M) n_M r_1^M p_2^M \left(1 - c \frac{N}{K_N}\right) \frac{M}{K_M}. \end{aligned}$$

Since the function  $F$  does not depend on  $M$ , the Jacobian is diagonal and so its eigenvalues are given by the diagonal entries,  $\partial F/\partial N$  and  $\partial G/\partial M$ .

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### C.1. TWO COMPETING SPECIES MODEL

### Coexistence Equilibria

The coexistence steady state  $(N^*, M^*)$  satisfies

$$\frac{N^*}{K_N} = 1 - \frac{1}{r_1^N p_2^N} \left\{ \frac{\alpha_N}{(1 - \beta_N)n_N} - p_1^N - r_2^N(1 - p_1^N - p_2^N) \right\} \quad (C.7)$$

$$\begin{aligned} \frac{M^*}{K_M} = 1 - \frac{1}{r_1^M \left(1 - c \frac{N^*}{K_N}\right) p_2^M} & \left\{ \frac{1 - (1 - \alpha_N) \left(1 - c \frac{N^*}{K_N}\right)}{(1 - \beta_M)n_M} - p_1^M \left(1 - c \frac{N^*}{K_N}\right) \right. \\ & \left. - r_2^M(1 - p_1^M - p_2^M) \right\} \end{aligned} \quad (C.8)$$

and substituting these into the Jacobian (C.6) gives eigenvalues

$$1 - (1 - \beta_N)n_N r_1^N p_2^N \frac{N^*}{K_N} \quad \text{and} \quad 1 - (1 - \beta_M)n_M r_1^M p_2^M \left(1 - c \frac{N^*}{K_N}\right) \frac{M^*}{K_M}$$

which are clearly less than 1 as long as

$$0 < (1 - \beta_N)n_N < 2 \quad \text{and} \quad 0 < (1 - \beta_M)n_M < 2. \quad (C.9)$$

Notice  $(1 - \beta_N)n_N$  is the maximum number of offspring a single  $N$  can rear in a year with unlimited food supply and under nest predation. At a steady population level,  $(1 - \beta_N)n_N$  has to be bounded above by 1 (otherwise the population would be growing) and it has to be larger than 0 (else the population would be in decline). A similar argument applies for the term  $(1 - \beta_M)n_M$  so that (C.9) is satisfied at the equilibria. Hence  $(N^*, M^*)$  is a stable equilibrium.

### Superior Competitor Only Equilibrium

Assuming the parameters are such that  $N^* > 0$  in (C.7) and  $M^* > 0$  in (C.8), i.e. coexistence is allowed, the eigenvalue  $\partial G(N^*, 0)/\partial M$  can be shown to exceed unity. The eigenvalue  $\partial F(N^*, 0)/\partial N$ , however, lies within the unit circle on the complex plane so that  $(N^*, 0)$  is a saddle point.

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#### C.1. TWO COMPETING SPECIES MODEL

### Inferior Competitor Only Equilibrium

Once more, assume the parameters allow coexistence. The steady state corresponding to inferior competitor only,  $(0, \hat{M})$ , is then given by setting  $N = 0$  in (C.4b) to obtain

$$\frac{\hat{M}}{K_M} = 1 - \frac{1}{r_1^M p_2^M} \left\{ \frac{\alpha_M}{(1 - \beta_M)n_M} - p_1^M - r_2^M(1 - p_1^M - p_2^M) \right\}. \quad (\text{C.10})$$

It can be shown that the eigenvalue of the Jacobian corresponding to  $\partial G/\partial M$  is less than unity whilst the eigenvalue corresponding to  $\partial F/\partial N$  exceeds unity and hence this steady state is also a saddle point.

### Extinction Equilibrium

Again, assuming the parameters allow coexistence, it is easily shown the Jacobian evaluated at  $(0, 0)$  has two eigenvalues exceeding unity implying this equilibrium is unstable.

### No Coexistence Equilibria

In the above analysis, the parameters were assumed to allow coexistence, i.e.  $N^*$  and  $M^*$  in (C.2b) and (C.4b), respectively, were in the positive quadrant. When this fails, the parameters may allow upto two steady states corresponding to single species persistence and complete extinction. For the case of single species persistence, the non-trivial equilibrium is easily shown to be stable while the equilibrium corresponding to extinction is unstable. When the parameters do not allow either species to persist the only steady state  $(0, 0)$  is obviously stable.

#### C.1.2 Parameter Estimation

All bar two of this model's parameters have been discussed in section 5.2.4. The remaining pair,  $K_N$  and  $K_M$  have a natural interpretation – simply denoting population carrying capacities. The manor in which these two values are employed in the modelling does not change whether the species persist or not at a given predation level. For



this reason, and since the model is not a quantitative description of the population dynamics, we shall set  $K_N = K_M = 1$ .

### C.1.3 Results of Alternative Heuristic Model

Again, for simplicity it is assumed that predation rates for both species of antbirds are the same; for bicolored and spotted antbirds this is a not unreasonable assumption (Willis, 1974). Figure C-1 shows in  $\alpha$ - $\beta$ -parameter space, for a range of other parameters, how the steady state solutions (C.2b) and (C.4b) are influenced by predation rates. The white regions correspond to competitive coexistence, the light grey corresponds to persistence of the subordinate competitor only, the dark grey to the dominant competitor only and the black region to extinction of both types.

Notice the revised model (C.1) gives rise to similar conclusions surrounding the rôle of predation as does the original model (5.2,5.8). Hence the precise manner competition is included in the model is most likely independent of the overall outcome.

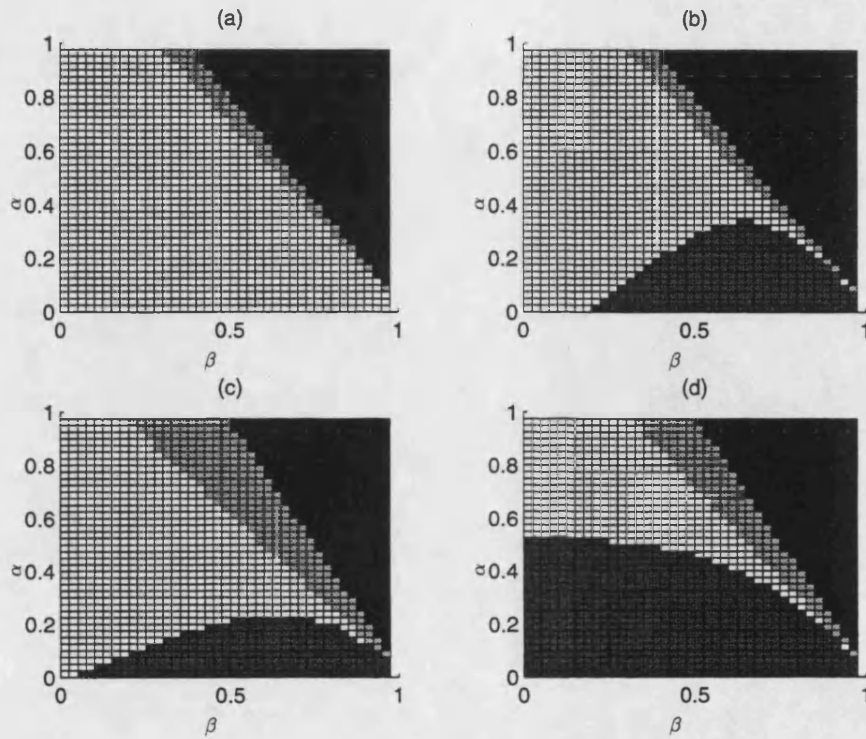


Figure C-1: The four regions in  $\alpha - \beta$  parameter space correspond to the four different equilibria. The black region corresponds to the case when neither bird can persist, the dark grey to the superior competitor only, the light grey to  $M$  only and the white corresponds to competitive coexistence. The other parameter values are (a)  $p_1^N = 0.2, p_2^N = 0.6, p_1^M = 0.2, p_2^M = 0.6, r_1^N = 0.4, r_2^N = 0.05, r_1^M = 0.5, r_2^M = 0.1, c = 0$ . (b)  $p_1^N = 0.2, p_2^N = 0.6, p_1^M = 0.2, p_2^M = 0.6, r_1^N = 0.4, r_2^N = 0.05, r_1^M = 0.5, r_2^M = 0.1, c = 0.3$ . (c)  $p_1^N = 0.2, p_2^N = 0.6, p_1^M = 0.2, p_2^M = 0.5, r_1^N = 0.3, r_2^N = 0.05, r_1^M = 0.8, r_2^M = 0.6, c = 0.3$ . (d)  $p_1^N = 0.2, p_2^N = 0.6, p_1^M = 0.2, p_2^M = 0.5, r_1^N = 0.4, r_2^N = 0.1, r_1^M = 0.8, r_2^M = 0.6, c = 0.5$ . In all cases  $K_N = K_M = 1$

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